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TECHNICAL REPORT EL-83-2

THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING SUBTIDAL MARINE AND ESTUARINE BENTHOS

by

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June 1983

Final Report

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REPORT DOCUMENTATION PAGE	READ INSTRUCTIONS BEFORE COMPLETING FORM

1. REPORT NUMBER Technical Report EL-83-2	2. GOVT ACCESSION NO. AD-A132 359	3. RECIPIENT'S CATALOG NUMBER

4. TITLE *(and Subtitle)* THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING SUBTIDAL MARINE AND ESTUARINE BENTHOS	5. TYPE OF REPORT & PERIOD COVERED Final report
	6. PERFORMING ORG. REPORT NUMBER

7. AUTHOR(s) David R. Kendall	8. CONTRACT OR GRANT NUMBER(s)

9. PERFORMING ORGANIZATION NAME AND ADDRESS U. S. Army Engineer Waterways Experiment Station Environmental Laboratory P. O. Box 631, Vicksburg, Miss. 39180	10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS

11. CONTROLLING OFFICE NAME AND ADDRESS Office, Chief of Engineers, U. S. Army Washington, D. C. 20314	12. REPORT DATE June 1983
	13. NUMBER OF PAGES 145

14. MONITORING AGENCY NAME & ADDRESS(if different from Controlling Office)	15. SECURITY CLASS. (of this report) Unclassified
	15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT *(of this Report)*

Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT *(of the abstract entered in Block 20, if different from Report)*

18. SUPPLEMENTARY NOTES

Available from National Technical Information Service, 5285 Port Royal Road, Springfield, Va. 22151.

19. KEY WORDS *(Continue on reverse side if necessary and identify by block number)*

Benthic habitat types	Unconsolidated soft bottoms	Substrate quality
Habitat parameters	Submerged aquatic vegetation beds	Temperature
Subtidal	Rock/hard bottoms	Current velocity
Estuarine	Reefs	Depth
Coastal marine	Salinity Vegetation quality	Water quality

20. ABSTRACT *(Continue on reverse side if necessary and identify by block number)*

This report represents a critical review of the literature on subtidal estuarine and coastal marine benthic habitats and the important measurable physical and chemical factors that influence community structure and production. It evaluates qualitative and quantitative trends in benthic community structure linked to physical and chemical environmental factors; it does not elaborate on the effects of important biological interactions such as competition and predation. -

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20. ABSTRACT (Concluded).

There are four generally recognized benthic habitat types within the subtidal estuarine and coastal marine environment. They are: (1) unconsolidated soft bottoms, (2) submerged aquatic vegetation beds, (3) rock/hard bottoms, and (4) reefs. Measurable habitat parameters known to influence the qualitative and quantitative structure of subtidal benthic communities associated with one or all of the four broad habitat types are: (1) salinity, (2) temperature, (3) other water quality descriptors (dissolved oxygen, turbidity, pollution), (4) substrate quality, (5) vegetation quality, (6) current velocity, and (7) depth.

There are many qualitative trends apparent in the literature concerning macroinvertebrate-substrate-water quality relationships. These are discussed, contrasted, and compared, with exceptions noted from different geographical areas of the east, west, and gulf coasts. The literature generally shows that quantitative correlations are usually obscured due to (1) natural biological variability, (2) the integrated influences of substrate and water physical-chemical conditions, and (3) biological interactions including competition and predation. Some site-specific quantitative relationships have been observed, but they are exceptions generally limited to intensively studied benthic species of commercial, recreational, or ecological importance, such as the hard clam. Detailed quantitative studies of the effects of multiple environmental factors on low-interest benthic infaunas are severely lacking or rare.

A review of physical-chemical parameters suggests that it is extremely difficult to isolate the effects on the benthos of one habitat descriptor such as substrate quality at the present state of the art. Much has been written concerning species-specific animal-substrate relationships, but many species are generalists and defy classification based on substrate quality alone. Therefore, the inherent complexity of environmental factors acting in concert to structure benthic communities makes it difficult to determine qualitative changes in benthic communities occurring within any given habitat type. Qualitative changes in benthic community structure may alter the trophic support value of the benthic habitat to bottom feeding fishes, but these changes cannot be accurately quantified using present substrate and water quality data and existing information on benthic invertebrate-substrate quality relationships.

PREFACE

This report furnishes U. S. Army Corps of Engineers District and field biologists with a contemporary critical review and synthesis document evaluating the role of physical-chemical factors in structuring subtidal marine and estuarine benthic habitats.

This document was prepared by Dr. David R. Kendall, Aquatic Habitat Group (AHG), Environmental Systems Division (ERD) of the Environmental Laboratory (EL), U. S. Army Engineer Waterways Experiment Station (WES). This work is a product of the Benthic Resources Assessment Technique (BRAT) Project under the Environmental Impact Research Program (EIRP). The project's Principal Investigator is Mr. John D. Lunz, AHG. Dr. Roger T. Saucier is the EIRP Program Manager; Mr. John Bushman is the Technical Monitor for this work at the Office, Chief of Engineers (OCE). This work was conducted under the supervision of Dr. Thomas Wright, Chief, AHG, Mr. Bob O. Benn, Chief, ESD, and Dr. John Harrison, Chief, EL. Critical reviews of this report were provided by: Mr. John D. Lunz; Drs. Donald F. Boesch, William D. Burbanck, Richard W. Heard, Terry McBee, Robin M. Overstreet, and Thomas D. Wright; and Mr. Bob O. Benn.

Commander and Director of WES during the conduct of this study and the preparation of this report was COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

Kendall, D. R. 1983. "The Role of Physical-Chemical Factors in Structuring Subtidal Marine and Estuarine Benthos," Technical Report EL-83-2, U. S. Army Engineer Waterways Experiment Station, Vicksburg, Miss.

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CONTENTS

CONVERSION FACTORS, INCH-POUND TO METRIC (SI)
UNITS OF MEASUREMENT

Inch-pound units of measurement used in this report can be converted to metric (SI) units as follows:

Multiply	By	To Obtain
dynes/square centimeter	0.1	pascals
Fahrenheit degrees	5/9	Celsius degrees or Kelvins*
feet	0.3048	meters
knots (international)	0.51444	meters/second
miles (U. S. statute)	1.609347	kilometers
parts per thousand (^{o}/oo)	1.0000	grams/liter

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* To obtain Celsius (C) temperature readings from Fahrenheit (F) readings, use the following formula: $C = (5/9)(F - 32)$. To obtain Kelvin (K) readings, use $K = (5/9)(F - 32) + 273.15$.

THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING
SUBTIDAL MARINE AND ESTUARINE BENTHOS

PART I: INTRODUCTION

1. U. S. Army Corps of Engineers construction and operational
activities may affect substrate quality in estuarine and marine coastal
environments. These substrate quality impacts directly affect benthic
organisms and indirectly affect fish (commercial, noncommercial, and
recreational or sport fish) dependent on the benthos for food. While
fish and shellfish have historically been considered valuable natural
resources, the extrinsic value of different benthic habitat types (and
their associated benthos) is difficult to quantify in terms that have
meaning to water resource planners attempting to evaluate substrate
quality changes. The Benthic Resources Assessment Technique (BRAT), a
methodology currently being developed by the U. S. Army Engineer Water-
ways Experiment Station (WES), will be used to quantify impacts of
Corps activities on fish habitat quality using information describing
benthic habitats in estuarine and marine coastal environments. The two
objectives of BRAT are to: (a) design an aquatic habitat classifica-
tion scheme, incorporating benthic ecological data, and (b) design an
aquatic habitat evaluation methodology.

2. An underlying assumption of BRAT, a method which will assign
"values" to different benthic habitats, is that one must first be able
to distinguish different benthic habitats. In many cases distinct
boundary areas for different habitat types are difficult to define due
to the gradual transition from one habitat type to the next and the
fact that most benthic environments exhibit patchiness within a rela-
tively small area. If the substrate and water quality conditions in-
fluencing the boundary definitions are understood, field sampling,
impact assessment, and construction and operations planning activities
can be conducted more economically and effectively.

3. Benthic organisms are rarely if ever distributed uniformly in

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time or space within a given aquatic environment. Individual benthic species exhibit seasonal life cycles and species-specific tolerances to environmental conditions. These largely determine their distribution spatially or temporally. Therefore, benthic species respond to environmental gradients and habitat patchiness and are distributed according to their individual ability to survive in any particular habitat type and water quality condition. Many studies have attempted to delineate the environmental and biological factors responsible for structuring benthic communities. Their results testify to the complexity of the relationships between the multiple environmental and biological factors and the folly of assuming simple correlations. Nevertheless, much has been learned concerning the distribution, composition, and secondary production of benthic communities.

4. This report summarizes the literature regarding benthic ecosystem structure and function. It shows the qualitative trends apparent in benthic invertebrate-substrate water quality relationships. It also shows the difficulty in quantifying the relationships between benthic invertebrates and substrate-water quality due to natural biological variability, biological interactions including predation and competition, and the integrated influences of substrate and water physical-chemical conditions.

Estuarine Environments

5. Estuarine environments broadly defined herein consist of all submerged (subtidal) benthic habitats, environments, and embayments that are usually semienclosed by land but have open, partly obstructed, or sporadic access to the open ocean, and in which ocean water is at least occasionally diluted by freshwater runoff from the land. This definition includes hypersaline bays, such as are found along the Texas coast, where the salinity may periodically be increased above that of the open sea.

6. Estuarine environments are bounded upstream by a zone in which the concentration of ocean-derived salts measures less than 0.5

parts per thousand (^{o}/oo)* during the period of average annual low flow, and downstream by an imaginary line closing the mouth of a river, bay, or sound. Salinity patterns observed in a given estuarine system are generally gradational, ranging from high open-ocean salinities greater than 30 ^{o}/oo near the mouth to less than 0.5 ^{o}/oo at the headwaters. Salinities commonly exceed 40 ^{o}/oo in hypersaline estuaries.

7. Large estuaries are best developed along the Atlantic and gulf coasts of the United States, while poorly developed on the Pacific coasts, where estuaries are more limited. Of the more than 500 estuaries in the United States, Chesapeake Bay represents the largest, ranging from 3 to 40 miles wide and 195 miles long. Along the Pacific coast of the United States, estuaries extend from Alaska south to San Francisco Bay. Glacier Bay, Puget Sound, Columbia River estuary, and San Francisco Bay represent the only sizeable estuaries found on the west coast; therefore, most of the examples and illustrations used to delineate benthic habitats and environmental factors that structure them will focus on the east coast and Gulf of Mexico estuarine system. Contrasts and comparisons among all areas will be made where applicable.

Coastal Marine Environments

8. Broadly defined, the marine coastal system considered in this report consists of those submerged benthic habitat types lying within the confines of the open ocean on the continental shelf and its associated high-energy coastline. These benthic environments are exposed to the waves and currents of the open ocean, and the ebb and flow of oceanic tides. Salinities generally exceed 30 ^{o}/oo with little or no dilution except outside the mouths of estuaries. This definition will also include coastal bays with no appreciable freshwater inflows which support typically marine benthic species and communities.

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* A table of factors for converting inch-pound units of measurement to metric (SI) units is found on page 3.

9. The marine benthic system boundary limits considered by this report extend from the outer edge of the continental shelf shoreward to the outer limits of the estuarine system near bays or inlets and to the low tide line along adjacent coastlines. For the purpose of this discussion, only submerged benthic habitat types will be considered.

10. Comparisons of similar habitats and their associated faunas from the east, west, and gulf coasts of the United States at comparable latitudes and depths have shown general patterns of species replacement within similar ecotypes, which approach the parallel community concept (Table 1-1) originated by Thorson (1957) whereby similar types of communities have been found existing at comparable latitudes and depths in similar bottom types. Temperature fluctuations on the east coast are primarily caused by seasonal shifts in strongly flowing air masses, whereas on the west coast temperature fluctuations are primarily brought about by upwelling and injections of cold water from the sea (Odum and Copeland 1974). The stress severity of temperature on the east coast is greater than that occurring generally on the west coast at similar latitudes, resulting in a more diverse fauna on the west coast than the east coast (Sanders 1968).

11. Parts II and III of this report discuss in detail the generally recognized benthic habitat types and those measurable physical and chemical environmental conditions affecting benthos structure and productivity in estuarine and coastal marine environments. These are briefly outlined below.

Benthic Habitat Types

12. A modification of the system proposed by the U. S. Fish and Wildlife Service in their publication "Classification of Wetlands and Deepwater Habitats of the United States" (by L. M. Cowardin, et al. 1979) has been used herein to broadly classify the aquatic systems and their major benthic habitats. The following benthic habitats have been generally recognized within each aquatic system.

Table 1-1

Examples of Species Replacement: West and East Coast Niche Substitutions,
Gulf Coast Equivalents, and Tropical Types when Stressed

(after Odum and Copeland 1974)

System Type	Description of Role	Tropical Stressed	Upper West Coast	Gulf Coast	Upper East Coast
Oligohaline river mouth	Clam with great capacity to burrow from cold and adapt to salinity variation		Mya arenaria	Rangia	Mya arenaria
Middle salinity estuary	Oyster reef niche	Crassostrea virginica	Ostrea gigas	Crassostrea virginica	Crassostrea virginica
	General crab carnivore, moving in and out of varying salinity	Callinectes	Dungeness crab Cancer	Blue crab Callinectes	Green crab Cancer
High-salinity estuary	Top carnivore in bottom irregularities	Lobster Panulirus	King crab Paralithodes	Stone crab Menippe	Lobster Homarus
Kelp system	Algal forests, bottom attached seaward of surf	--	Macrocystis	--	Laminaria
Beach and surf	Deep digging clam adapted to heavy energies just seaward of breakers	Spisula	Razor clam Siliqua	Spisula	Surf clam Spisula
	Surf zone sand dollar	Mellita	Dendraster	Mellita	Echinarachnius
Intertidal rocks*	Grazers of intertidal rocks, periwinkles	Littorina ziczac	Littorina planaxis Littorina scutellata	Littorina irrorata	Littorina litorea
	Intertidally protected filter feeders barnacles, Ulva	Balanus amphitrite Ulva	Gooseneck barnacle Ulva	Balanus eburneus Ulva	Balanus balanoides Ulva
Coastal plankton	Zooplankton-eater	Anchovy	Pacific herring, Sardines	Menhaden, Threadfin	Atlantic herring, Alewives

* Hedgepeth (1953, 1967).

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Unconsolidated soft bottom

13. The unconsolidated bottom habitat type includes soft bottom habitats characterized by the lack of a stable surface for plant and animal attachment. This habitat type is generally found in lower energy environments than rock/hard bottoms, and may be unstable because of currents, tidal flows, and wave activity. The substrate characteristics (grain size, mineralogy) of soft bottom habitats in estuarine and marine coastal environments is largely a function of the sediment source and current velocity. Substrate types in unconsolidated soft bottom habitats include (a) gravel, (b) shell-sand, (c) sand, (d) mud, and (e) organic. Mud substrates may include admixtures of sand, silt, clay, shell, and organic material, although the finer particle sizes (silt and clay) usually predominate. Organic substrates are usually characterized by high organic content and strongly reducing conditions. Cobble-gravel and sand substrates are usually well oxygenated, while mud and organic habitats are characteristically oxygen deficient. Organic sediments with large concentrations of organic matter usually support an impoverished benthic community of low diversity.

Submerged aquatic vegetation bed

14. The submerged aquatic vegetation bed habitat type is characterized by rooted vascular plants (seagrasses, e.g. eelgrass and turtle grass) and macroalgae (kelp) attached to or rooted in the rock/hard bottom or unconsolidated soft bottom substrate. These vegetated substrates provide protection and a rich food supply for associated macroinvertebrate infaunal and epifaunal communities and are characteristically very productive benthic habitats.

Rock/hard bottom

15. The rock/hard bottom habitat type includes submerged benthic habitats with substrates consisting predominantly (75 percent or more) of stones, boulders, or bedrock which are unvegetated, or where vegetation covers less than 30 percent of the rock surface. This habitat also includes hard compacted clay bottoms which provide suitable substrates for sessile benthos. The stability of this type of benthic habitat allows for a rich diversity of generally sessile benthic

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species (faunas and floras) to develop. This habitat type is usually characterized by high physical energy and saturated or nonsaturated dissolved oxygen conditions in surrounding waters. For purposes of this document, rock/hard bottom habitats will also include "artificial reefs" formed by the placement of man-made structures (tires, sunken vessels, etc.) which provide relief and a hard substrate for benthos.

Reef

16. The reef habitat type is characterized by ridgelike or moundlike structures formed by the colonization and growth of sedentary invertebrates. These structures are usually elevated above the surrounding substrate and tend to interrupt normal wave or current patterns. Biologically formed reefs found in estuarine environments are mollusk (oyster) and worm (sabellariid) reefs. Marine coastal reefs include coral and sabellariid reefs. The distribution of coral reefs is limited to tropical and subtropical marine environments.

Habitat Descriptors

17. Each habitat type will be discussed in terms of measurable habitat descriptors important to the structure and productivity of benthic macroinvertebrate communities. In estuarine and marine coastal environments, these descriptors include hydrologic regime affected by depth, currents, and wave energies and various parameters describing substrate, vegetation, and water quality, including salinity and temperature.

PART II: ESTUARINE AND MARINE BENTHIC HABITATS

18. The following four submerged benthic habitats are described in this section.

    <u>a</u>. Unconsolidated soft bottom

    <u>b</u>. Aquatic vegetation bed

    <u>c</u>. Rock/hard bottom

    <u>d</u>. Reefs

These are generally recognized as discrete habitats within estuarine and coastal marine environments. Distinctions between variant estuarine and marine habitat examples are illustrated where appropriate, although some may overlap in both systems to some extent. In the following chapter measurable habitat descriptors affecting the distribution, composition, and production of benthos within each habitat type are discussed and evaluated.

Unconsolidated Soft Bottom Habitats

19. On a spatial basis, unconsolidated soft bottom habitats make up the largest complex of subtidal benthic habitat types in estuarine and marine environments (Figure 2-1). Soft bottom habitats have been the object of much study, particularly with regard to animal-sediment relationships or community-sediment classifications. Ecologically distinct benthic communities have been described for marine soft bottom environments (Peterson 1913; Thorson 1957, 1958). Distinct community patterns have been delineated in the temperate marine coastal environment at comparable latitudes and varying depths (i.e., Parallel Communities (Thorson 1957)), although the distinct community dominance hierarchies observed at temperate latitudes do not appear to hold for warm temperate or tropical regions because of low dominance and high species evenness and diversity (Thorson 1971). Early investigators (Peterson 1913, Thorson 1957) have characterized sublittoral marine soft bottom habitats as being physically homogeneous, although recent studies have shown that the level bottom is "spatially heterogeneous,

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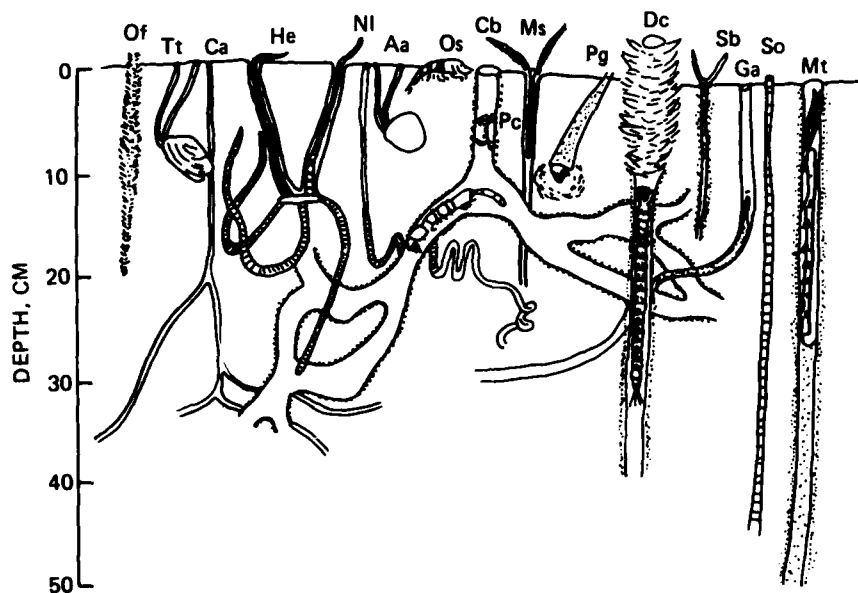
Figure 2-1. Vertical distribution of dominant macrobenthic species from
the Georgia nearshore subtidal shelf environment. Legend: Aa = *Abra
aequalis*; Ca = *Capitomastus* cf. *aciculatus*; Cb = *Callianassa biformis*;
Dc = *Diopatra cuprea*; Ga = *Glycera americana*; He = *Hemipolis elongata*;
Ms = *Megelona* sp.; Mt = *Mesochaetopterus taylori*; Nl = *Notomastus
latericeus*; Of = *Owenia fusiformis*; Os = *Oxyurostylis smithi*;
Pc = *Pinnixa chaetopterana*; Pg = *Pectinaria gouldi*; Sb = *Spiophanes
bombyx*; So = *Spiochaetophterus oculatus*; Tt = *Tellina* cf. *texana* (after
Dörjes and Howard 1975)

and consists of biologically produced microlandscapes" (Rhoads 1974).
Comparable community delineations by substrate type (cobble-gravel,
shell/sand, sand, mud, organic) are more difficult to establish in
estuarine soft bottom environments due to marked patchiness in sediment
quality and environmental gradients (fluctuations in salinity and tem-
perature) along the axis of the estuary. In poikilohaline estuaries
(estuaries having highly variable salinity), animal-sediment relation-
ships may be difficult to define due to overriding effects of variable
salinity on faunal composition and distribution within a given sub-
strate type (e.g. sand). Dörjes and Howard (1975) concluded in a study
of animal-sediment relationships along an environmental gradient in the

Ogeechee River estuary in Georgia that "the dependence upon sediment texture is superseded by dependences on salinity" and were forced to classify the distribution of benthic communities in this estuary based on salinity rather than sediment classification. However, a recent study by Burbanck (1981) in a poikilohaline subestuary in Delaware Bay, successfully classified infaunal groups based on their fidelity to and association with coarse-grained and fine-grained sediments. In relatively homeohaline environments with stable salinity fluctuations, animal-sediment relationships may be more easily defined. Sanders (1958, 1960) found relatively distinct animal-sediment relationships for macrobenthos in Buzzards Bay, Massachusetts, where salinity fluctuations were minimal (29.5-32.5 ^{o}/oo). His studies showed that filter feeding infaunas were primarily associated with sand bottoms, while deposit feeding infaunas were primarily associated with muddy sediments. Sanders (1956) in a study of animal-sediment relationships in Long Island Sound found bottoms with silt-clay fractions in excess of 50 percent supported fewer individuals and species than coarser sediments. He found that substrates between 25 and 50 percent silt-clay were likely to support an abundance of deposit feeders, while coarser sediments less than 25 percent silt-clay supported the largest community with high concentrations of suspension feeding benthos. Similar animal-sediment relationships were also found in a poikilohaline estuary by Burbanck (1981). Rhoads and Young (1970) observed a similar segregation of deposit feeding and filter feeding benthos, and their study showed that deposit feeding benthos were able to exclude or inhibit the settlement of filter/suspension feeding benthos by creating an unstable, easily resuspended layer of biologically reworked sediments. They suggested that sediment instability and water turbidity maxima near areas of major deposit feeding aggregations successfully excluded suspension feeding groups, which suggestion they called the "Trophic Group Amensalism Hypothesis." Studies in a subtropical estuary (Bloom, Simon, and Hunter 1972) and a tropical lagoon (Aller and Dodge 1974) have confirmed the general validity of this hypothesis at lower latitudes.

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20. Another factor complicating animal-sediment relationships on soft bottoms, especially relatively shallow ones (less than 20 m deep), is the relative instability of these habitats compared to vegetated bottoms, rock/hard bottoms, and reef habitats. Storms and seasonal changes in the amount of freshwater inflow modify estuarine sediment composition and benthic community structure by eroding or depositing sediments; benthic fauna associated with unconsolidated soft bottom habitats are thereby continually disrupted by changing sediments within their environment. Seascape features such as sand waves, ripple marks, and a low level of bioturbation indicate a general instability of bottom sediments and their subsequent movement over the bottom which displaces and disrupts marine benthic communities. Relatively shallow, nearshore shelf benthic environments are subject to a greater frequency of disturbance than deeper midshelf-to-shelf edge benthic environments. Disturbances may be in the form of climatic variability (salinity, temperature, turbidity, etc.) and/or physical disruption of the bottom from currents, waves, dredging activities, and biological disturbance (Howard, Mayou, and Heard 1977; Dayton and Hessler 1972). Benthic faunas associated with shallow unconsolidated soft bottom habitats are continually being disrupted by changing sediments within their environment due to localized bathymetry and hydrographic conditions. Johnson (1972) has proposed an ecologically realistic concept of a benthic community as "a temporal and spatial mosaic, parts of which are at different levels of succession." From this viewpoint "the community is a collection of relics of former disasters." Therefore, it is not surprising that shallow sublittoral benthic infaunal communities rarely show close animal-sediment relationships over broad areas for a given habitat type and species, although they may show broad relationships for functional trophic groups as indicated by the Trophic Group Amensalism Hypothesis.

21. Studies of marine benthic community structure in shelf environments indicate that faunal changes occur along a continuum from nearshore to deepwater environments and that these changes are primarily related to bathymetric zones rather than to sediment compositional

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changes (Day, Field, and Montgomery 1971; Buchanan, Sheader, and Kingston 1978; Flint and Holland 1980). In general, transect studies of shelf benthos from the east coast and Gulf of Mexico have shown that density and standing crops decrease from shallow to deep water, while species richness, species diversity, and equitability (lack of dominance) increase (Sanders 1968, Sanders and Hessler 1969; Day, Field, and Montgomery 1971; Flint and Holland 1980; Parker 1964; Boone, Granat, and Farrell 1978). Broad latitudinal studies of marine soft bottom benthic communities have found a general decrease in benthic standing crop biomass with latitude in relatively shallow nearshore environments (Emery and Uchupi 1972).

22. An intriguing discussion of soft bottom benthic community dynamics and production that has recently surfaced is based on the frequency of disturbance or perturbation. Benthos inhabiting muddy soft bottom habitats subjected to frequent disturbance (storms, current scour, dredged material disposal, environmental stress, etc.) characteristically differ markedly in their life history strategies from those infaunal benthos from relatively stable, undisturbed habitats; the former are called "opportunistic species" (Grassle and Grassle 1974), while the latter are termed "equilibrium species" (McCall 1977, 1978). Opportunistic species recolonizing muddy sediments after a disturbance are generally surface deposit feeders or suspension feeders living in the near-surface sediment layer. These fauna are generally small in size, exhibit erratic population density cycles caused by high reproductive potential (continuous recruitment), high mortalities, and short life spans. Equilibrium species may be deposit feeders or suspension feeders usually living deep within the sediment: they are generally larger in size, long lived, and have lower reproductive potentials (seasonal reproductive cycles) and planktotrophic larvae. Opportunistic species are better equipped to recolonize recently disturbed areas quickly due to their higher reproductive potential and life history strategies, whereas equilibrium species usually take much longer. Opportunistic species are also generally eurytopic (ubiquitous) compared with equilibrium species. This characteristic enables them to survive

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in environmentally stressful or marginal environments. Table 2-1 illus-
trates the adaptive strategies of opportunistic species versus equi-
librium species. Thus, the frequency of disturbance for a given sedi-
ment habitat type will influence the type of infaunas associated with
that sediment type. Figure 2-2 illustrates the continuum of faunal
structure over time and distance following a physical or pollution dis-
turbance. The gross similarities of faunal structure are readily ap-
parent between the two types of disturbances, illustrating the tendency
for equilibrium-type species to be displaced and replaced by more eury-
tolerant opportunistic species following a perturbation. This figure
also shows the succession of benthos and concomitant changes in the
sediment oxidized layer from the pioneer community (opportunistic
species) to the climax community (equilibrium species).

Table 2-1

Benthic Adaptive Strategies (after McCall 1977)

Disturbed Habitats	Undisturbed Habitats

1. Opportunistic species
   a. Many reproductions *per year*
   b. High recruitment
   c. Rapid development
   d. Early colonizers
   e. High death rate
	1. Equilibrium species
	   a. Few reproductions per year
	   b. Low recruitment
	   c. Slow development
	   d. Late colonizers
	   e. Low death rate

2. Small size	2. Large size
3. Sedentary	3. Mobile
4. Deposit feeders (mostly surface feeders)	4. Deposit and suspension feeders
5. Brood protection; lecithotropic larvae	5. No brood protection; planktotrophic larvae
6. Eggs/female = 10-10^3	6. Eggs/female = 10^3-10^6

23. Generally speaking, the composition of sediments found in
estuaries reflects the source of sediments (terrigenous or carbonate),
bathymetry, and hydrography of the particular estuarine system. The
distribution of sediments reflects the subtle changes in currents

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OPPORTUNISTIC SPECIES   EQUILIBRIUM SPECIES
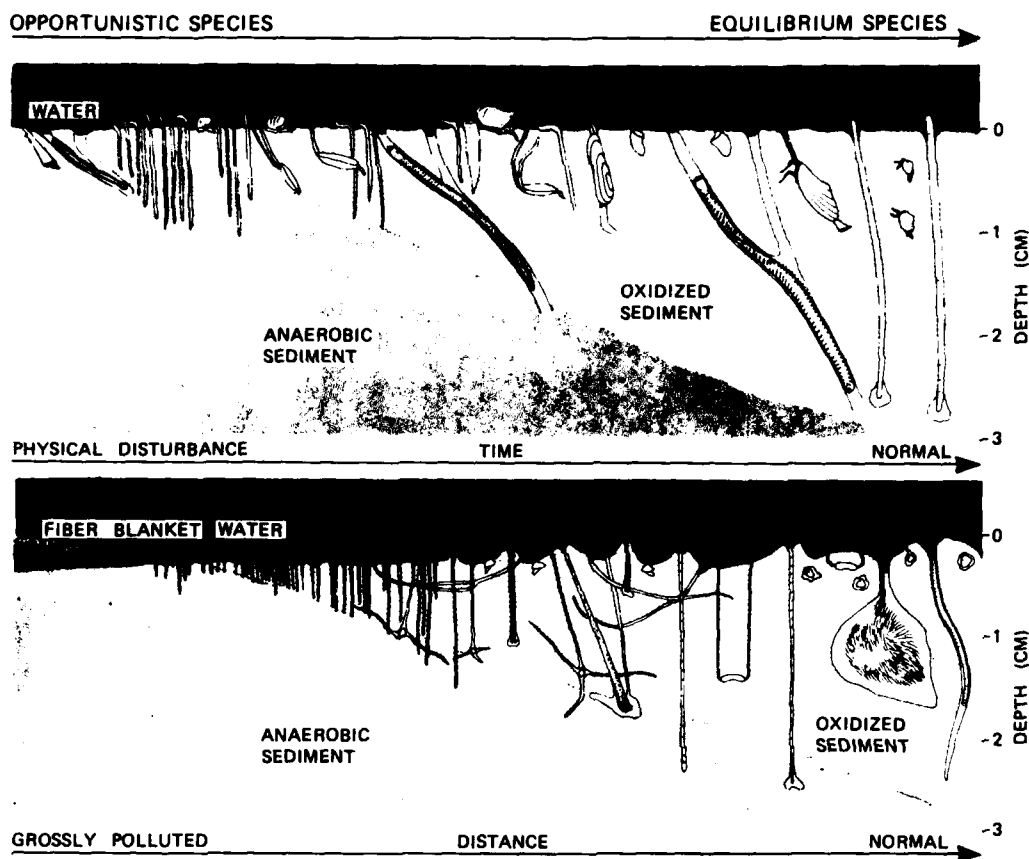
Figure 2-2. Unconsolidated soft bottom community continuum along
a physical disturbance time scale and pollution distance gradient
(after Rhoads, McCall, and Yingst 1978)

(tidal, wind generated, seasonal river flow) entering or leaving the
system, all of which affect the quality and quantity of the associated
benthos. Figure 2-3 shows the significance of bottom type and its
covariable, current velocity, as they affect the distribution of the
quahog (*Mercenaria mercenaria*) in a Maryland estuary.

24. Types of unconsolidated soft bottom habitats generally rec-
ognized based on sediment size classification are (a) gravel, (b) shell/
sand, (c) sand, (d) mud, and (e) organic. All are indirectly related
to current velocity and wave activity within each system. None of the
categories of sediment are entirely distinct entities; each type grades

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A) BOTTOM, TYPE

B) CURRENT, KNOTS

MUD

SAND-MUD MIXTURES

SAND

SHELL

1   2   3

AVERAGE DENSITY, N/M^2

INSIGNIFICANT

0.1

0.2-0.5

0.6-1

1   2

AVERAGE DENSITY, N/M^2

Figure 2-3. Relationship of the average density of *Mercenaria mercenaria* versus (a) bottom type; and (b) current velocity in Chincoteague Bay, Maryland (after Wells 1957)

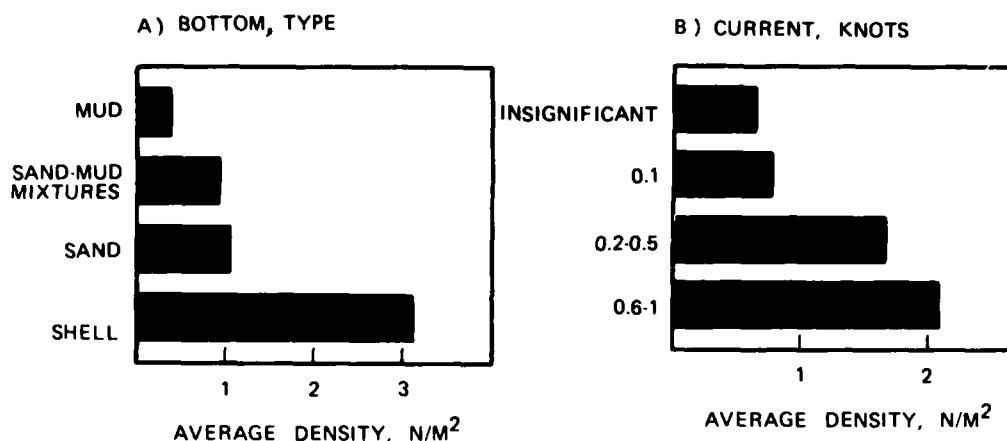into the next size category in a continuum based on varying admixtures of clay, silt, sand, shell, and organic matter contents, thereby making distinctions between gross habitat types difficult unless some objective classification scheme is used. Soft bottom infaunal species are rarely found distributed entirely or exclusively within any given sediment type; they are usually distributed along a gradient of varying sediment compositions (soft bottom habitat type), exhibiting peak abundances within a given sediment type, or they may be relatively ubiquitous with no discernible sediment affinities.

Submerged Aquatic Vegetation Beds

25. Aquatic vegetation beds are an important and distinct benthic habitat type in estuaries and marine coastal environments worldwide. The distribution of submerged aquatic vegetation is governed by temperature (depending on both latitude and season), salinity, substrate quality, currents, water quality, and bathymetry (depth). Submerged aquatic vegetation habitats found in estuarine and marine coastal environments are principally of two types: (a) rooted vascular plants (seagrasses) and (b) attached macroalgae (kelps). For purposes of this

discussion, macroalgae will be limited to those types forming quanti-
tatively distinct zones in estuarine and marine coastal environments,
such as the kelps (Phaeophyta).

Rooted vascular plants

26. Rooted vascular plants such as seagrasses are worldwide in
distribution in shallow coastal and estuarine waters, in unconsolidated
soft bottoms for the most part. They are very important habitats due
to the protection they provide from erosion; their role in sediment
accretion and stabilization; their high productivity; and their use as
refuges and nursery and spawning areas by many commercial, recreational,
and ecologically important species (Phillips 1980).

27. Seagrasses are flowering plants (Class: Monocotyledonae).
Some 45 species have been described worldwide (Phillips 1980). In
tropical to subtropical regions of the western Atlantic (i.e., from the
Gulf of Mexico to North Florida on the Atlantic Coast) the dominant
species is turtle grass, *Thalassia testudinum*. Other species from this
same region are the shoal grass, *Halodule wrightii*; manatee grass,
Syringodium filiforme (Cymodocea); and widgeon grass, *Ruppia maritima*.
In temperate regions, the number of seagrass species diminishes. Of
the five species reported, only two are significant, and they are eel-
grass, *Zostera marina*, and widgeon grass. Both of these species are
distributed widely along the Atlantic and Pacific coasts.

28. In oligohaline to freshwater zones of estuaries that are
tidally influenced, other rooted vascular plants may be found, which
also form extensive aquatic vegetation beds. A few species such as the
tapegrass (*Valliseria americana*) and the exotic eurasian watermilfoil
(*Myriophyllum spicatum*) are known to support high densities of fresh-
water and estuarine animals (Burbanck and Burbanck 1967, Burbanck and
Burbanck 1979, and Menzie 1980). Both species have a wide distribution
in the eastern United States and have been reported in tidally influ-
enced reaches of east coast and gulf coast estuaries (Burbanck and
Burbanck 1967; Burbanck and Burbanck 1979; Radford, Ahles, and Bell
1968; Tarver et al. 1979; Menzie 1980; Desselle et al. 1978).

29. Rooted vascular plant species are almost exclusively found

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on unconsolidated muddy sand bottoms, thus occupying a habitat virtu-
ally uncontested by benthic algae except for a few green algal families
(Codiaceae and Caulerpaceae) in the tropics (Phillips 1978). However,
two species of "surf grasses," *Phyllospadix torreyi* and *Phyllospadix
scouleri* grow on rocky substrates down to 50 ft along the Northeast
Pacific Coast; the latter species being distributed from Vancouver
Island south to Mexico (Dawson 1956, Phillips 1978).

30. Subtropical and tropical seagrasses occur in waters of mod-
erate current energy between 0.6- and 20-m depth in Puerto Rico, the
Florida Keys, and south Texas (Odum 1974, Zieman 1975). In tropical
areas of higher wave energy, seagrasses are displaced by coral and
algal reef systems. This is due in part to adaptations to lower light
intensities and currents and grazing by reef-associated animals (sea
urchins, fish, etc.). Turtle grass requires high light intensity, and
the maximum depth of large beds is generally around 10 m. *Thalassia* is
considered to be a tropical marine plant, favoring relatively stable
salinities from 20-35 ^{o}/oo and temperatures in the northern Gulf of
Mexico ranging from 17° to 32° C (Zieman 1975, Phillips 1978). *Halodule*
is much more euryhaline, having been reported from both hypersaline
estuaries in Texas (Odum 1974) and lower salinity environments (Thorhaug
1981). This species appears to be primarily restricted to very shallow
or lower salinity environments. This may be a consequence of its poor
competitive ability with turtlegrass (Thorhaug 1981) or to its physio-
logical adaptability in these environments. Widgeon grass *(Ruppia)* is
also primarily restricted to low-salinity areas. Studies of turtle
grass have shown that environmental factors are primarily responsible
for blade (leaf) densities, standing crop biomass, and production
within marine coastal environments (Zieman 1975).

31. Eelgrass forms the single most important temperate seagrass
species. On the Pacific coast eelgrass extends from Port Clarence,
Alaska (lat. 65° N), as far west as Atka Island (long. 175° W) and as
far south as Agiopampo Lagoon, Mexico (lat. 26° N)(Phillips 1974). On
the Atlantic Coast of North America, eelgrass extends from Hudson Bay,
Canada, the southern tip of Greenland, and one locality in Iceland

(lat. 65° N) to Beaufort, North Carolina (Phillips 1974, Penhale and
Smith 1977).

32. Eelgrass is a relatively eurytopic species, surviving the
temperature range of 5° to 27° C, and salinities ranging between 10 and
30 ^{o}/oo are optimum for growth (Phillips 1974). *Zostera* activity has
been correlated with temperatures and photoperiod, and both appear to
be responsible for controlling growth and regulating reproduction in
this species (Phillips 1974). Eelgrass occurs on tidal mud flats and
in bays and estuaries at depths up to 5.4 m in turbid water and 30 m in
clear water (Phillips 1974), although the general limit of dense eel-
grass beds is 12-15 m in clear water. Along the open southern Cali-
fornia Coast, eelgrass is often found on sandy bottoms in depths of 5 m
or more. Substrate preferences for this species range from firm sand
to soft mud, and distributions are apparently affected by current and
wave energies and storm surges. Moderate currents of up to 3.5 cm/sec
appear to enhance eelgrass growth, and the most luxuriant growth occurs
within this range (Phillips 1980).

33. Representative annual production values for seagrasses range
from 125 to 4000 g C/m^2/year for turtlegrass, and 50 to 950 g C/m^2/year
for eelgrass (Phillips 1980). Table 2-2 illustrates some regional an-
nual production estimates for representative seagrass species, and it
is readily apparent that overall turtlegrass is approximately twice as
productive as eelgrass (1000 g C/m^2/year for subtropical seagrasses ver-
sus 480 g C/m^2/year in temperate seagrasses) (McRoy and McMillan 1977).

34. This discrepancy may largely be a function of the length of
the growing season (250 days for turtlegrass versus 120 days for eel-
grass) (McRoy and McMillan 1977). Subtropical seagrass beds along the
coast of Florida generally show a much less pronounced seasonal growth
pattern due to less variable temperature and light intensity. Rooted
aquatic vegetation such as eelgrass and turtlegrass are considered to
be the chief producers of organic matter in shallow sublittoral waters
(Carriker 1967). Eelgrass has been shown to be capable of pumping
nutrients from subsurface sediments to surface waters, where they are
exported, and it is likely that other seagrass species function in a

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Table 2-2

Comparative Average Productivities of Selected Seagrasses

(After McRoy and McMillan, 1977)

Species	Locality	Productivity g C/m^2/day	Annual Productivity g C/m^2
Seagrasses			
Thalassia testudinum	Puerto Rico	2.4-4.5	600-1125
(assume growing	Florida	0.35-16	88-4000
season of 250 days)	Texas	0.9-9.0	225-2250
Halodule wrightii (assume growing season of 120 days)	North Carolina	0.48-2.0	72-240
Zostera marina	Denmark	2.0-7.3	240-1095
(assume growing	Rhode Island	0.4-2.9	60-435
season of 120 days)	North Carolina	0.2-1.7	30-255
	Washington	0.6-4.0	90-600
	Alaska	3.3-8.0	495-1200
Epiphytes on seagrasses			
Zostera marina	Massachusetts	--	20[a]
	North Carolina	--	73 (Detritus)[b]
Thalassia testudinum	Florida	--	200[c]

[a] After Marshall 1970.
[b] After Penhale and Smith 1977.
[c] After Jones 1968.

similar manner (McRoy and Barsdate 1970). Studies by Penhale and Smith (1977) indicate that as much as 15 percent of the total dissolved organic carbon (DOC) in the estuarine system near Beaufort, North Carolina, may be contributed by eelgrass and its associated epiphytes. The significance of seagrasses as a source of organic carbon has also been documented for the eastern Gulf of Mexico coastal zone (Iverson et al. 1979).

35. Epiphytes associated with seagrass ecosystems have been found to contribute substantial amounts of carbon (Table 2-2). Den Hartog (1970) has recorded 200 algal epiphyte species from turtlegrass, while Davis (1911) reported 42 species of epiphytes from eelgrass beds from Woods Hole, Massachusetts. Estimates of epiphyte production

within seagrass ecosystems range from 20 percent of the mean annual net production of turtlegrass in Florida (200 g C/m^2/year) (Jones 1968) to 25 percent of the annual production of eelgrass in North Carolina (Dillon 1971). A highly diverse faunal community is distributed within the seagrass substrate (infauna) or on the seagrass blades as encrusting or motile invertebrates (epifauna). Numbers of invertebrate species reported from tropical to subtropical seagrass communities range from 75 (stressed community) to 230 species, and 112 to 138 species in temperate eelgrass communities (O'Gower and Wacasey 1967, Young and Young 1977, Stoner 1980, Marsh 1973, Orth 1973, Phillips 1974). Studies by Burbanck and Burbanck (1967, 1979) and Menzie (1980) have also shown rooted aquatic vegetation beds in upper reaches of estuaries to be significant habitats for many freshwater and estuarine invertebrates. Seagrass communities are usually characterized as supporting a detritus-based food web, and relatively few animal species graze the seagrass blades directly (Phillips 1980). MacGinite (1935) in a quantitative study of trophic relationships of California seagrass communities found 95 percent of the species by weight to be detritus feeders.

Kelp beds

36. Large brown algae called kelp inhabit shallow marine waters of temperate zones of both the northern and southern hemispheres. Kelp are usually found seaward of the surf zone to depths less than 31 m, or in high salinity embayments with some swell and low-turbidity clear water (Figure 2-4). Kelp grows to 50 m in length on the Pacific Coast, with optimum growth occurring at water depths of 8-30 m. *Nerocystis*, an annual species, may reach lengths of 30 m in a single year (Thorson 1971). Another important genus, *Macrosystis* (giant kelp), is a perennial and grows to even greater lengths. Kelp beds may be 5 km wide along coasts, where they act as a protective buffer along marine coastal shallow water environments breaking up waves and subduing currents, thereby protecting shorelines from erosion. They grow as vertical standing underwater forests that wave and lash with the motion of the sea, supporting an immense production of associated epiphytes and invertebrates. The giant kelp is found on the Pacific Coast of North

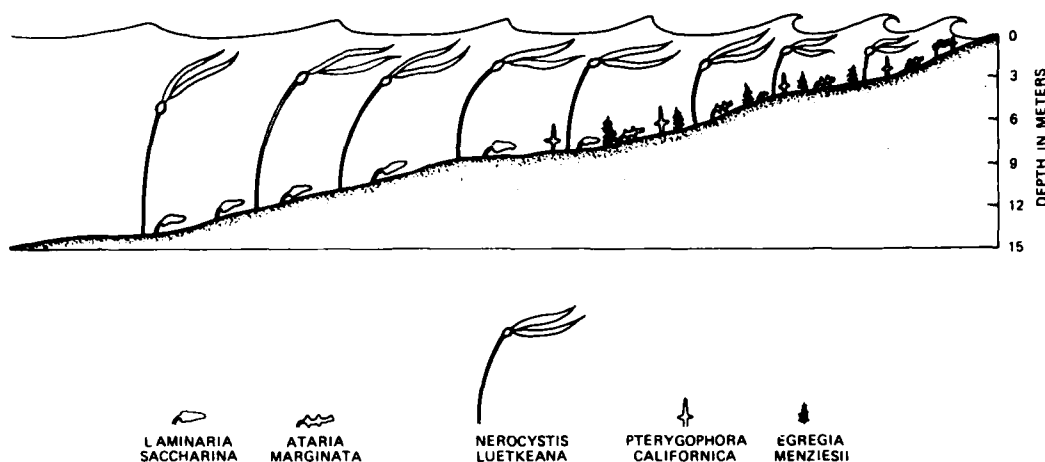| L AMINARIA SACCHARINA | ATARIA MARGINATA | NEROCYSTIS LUETKEANA | PTERYGOPHORA CALIFORNICA | EGREGIA MENZIESII |

Figure 2-4. Schematic of a "typical" kelp bed in Puget Sound.
Highly generalized representation of dominant kelp species.
Horizontal axis and plant densities not to scale (after
Phillips 1974)

America from lat. 27° N (west coast of Baja, California) to the Monterey
Peninsula, California, and tolerates temperatures from 0° to 18° C, and
salinities from 26.3-43.7 °/oo. Kelp beds exhibit maximum development
on hard rock bottoms and cool waters of the west coast. On the rocky
temperate western Atlantic coast, *Laminaria* serves as a dominant kelp
species. *Laminaria* may also dominate kelp beds on the Pacific coast.
Other macroalgae make up significant portions of the kelp system and
may be quantitatively significant as microhabitats for macroinverte-
brates in the absence of the larger kelp dominants, as illustrated by
Table 2-3. This table shows that sessile benthos may reach enormous
biomass densities within algae/kelp beds. Some 114 algal species have
been reported from giant kelp beds (Dawson, Neushul, and Wildman 1960).
Production of giant kelp has been estimated at between 448 to 3138 g/m^2/
year averaging 1464 g/m^2/year (dry-weight-organic matter) (Phillips
1974). Production of kelp is therefore similar in magnitude to coral
reefs, freshwater springs, and seagrass systems (Phillips 1974). In
contrast to seagrass systems, where the principal food web is detritus
based, kelp systems exhibit both a grazing and detritus-based food web.

Table 2-3

Comparison of the Standing Crops of the Chief Attached Plants and

Sessile Animals from Two Locations*

Classification	Under Canopy			Not Under Canopy			Mean Not Under Canopy* / Mean Under Canopy
	Frequency	Range** g/m^2	Mean** g/m^2	Frequency	Range** g/m^2	Mean* g/m^2	
Phaeophyceae							
Cystoseira	1.0	22-281	90	1.0	25-436	200	2
Egregia	0	0	0	0.1	0-4	0.4	--
Eisenia	0.1	0-22	2	0.3	343-1865	405	200
Laminaria	0.2	0-52	6	1.0	2.3-1758	539	90
Juvenile							
Macrocystis	0	0	0	0.8	P†-5.8	0.9	--
Pterygophora	1.0	0.4-517	124	0.7	163-4258	1263	10
Rhodophyceae							
Fleshy reds	0.6	0-25	6	1.0	0.5-476	222	37
Calcareous reds	1.0	114-366	209	1.0	281-940	658	3
All algae††	1.0	285-1058	469	1.0	810-6688	3145	7
Sessile animals	1.0	193-923	508	1.0	129-999	506	1

* One site was well beneath a dense *Macrocystis* canopy, which had been in existence for approximately a year, while the other site, 30 m away, extended out from the edge of the canopy and was free from any shading effects.

** Mean values, ranges, and frequencies were computed from ten samples of area 1 m^2, positioned randomly within the sampled location.

† P = present but less than 0.1 g.

†† Does not include adult *Macrocystis* or *Lithothamnion* (after North 1964).

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Herbivores (e.g. sea urchins) are common and may be destructive to the kelp bed habitat. Kelp and associated algae serve as substrates and food for many sessile encrusting and motile invertebrates. Densities of motile invertebrates of up to $100,000/m^2$ on blade surfaces of giant kelp have been reported by Wing and Clendenning (1959). Kelp blade surfaces are also generally heavily encrusted with bryozoans, hydroids, and other sessile species. Kelp beds also serve as critical foraging and reproductive habitats for many important commercial species such as lobster, abalone, crabs, and fish.

Rock/Hard Bottom Habitats

37. Estuarine distributions of hard bottom habitats are limited to areas where currents and waves are sufficient to maintain a surface free of sediment. Rocky substrates, oyster reefs, shell deposits, and other hard surfaces such as compacted clay bottoms seldom exist as clean surfaces in estuaries because of generally high rates of sedimentation (Day 1959, Percival 1929). Organisms attempting to settle must usually contend with sediment layers varying in thickness on top of hard surfaces (Carriker 1961). These habitats serve as "terra firma" for sessile macroinvertebrate communities sometimes referred to as "fouling communities." Fouling communities associated with hard bottom estuarine habitats are comprised of dominant sessile species such as mussels, bryozoans, barnacles, sea anemones, sea whips (e.g. *Leptogorgia*), hydrozoans, sponges, and tunicates *(ascidians)*. These species in turn serve as substrates and microhabitats for many associated cryptic, motile, and boring organisms. Filter/suspension feeding is the primary trophic activity or mode of feeding for the dominant species groups within these communities. Epifaunal macroinvertebrates dominate these communities and are subjected to greater diel environmental stresses than infaunal communities inhabiting unconsolidated soft bottom habitats. Typical fouling communities are often contiguous with oyster communities, where relative proportions of dominant species contribute the only discernible differences.

38. Marine rock/hard bottom habitat. Marine hardgrounds exhibit wide but patchy distributions on Pacific, Atlantic, and Gulf shelf environments bordering the United States (Figure 2-5). Rocky substrates
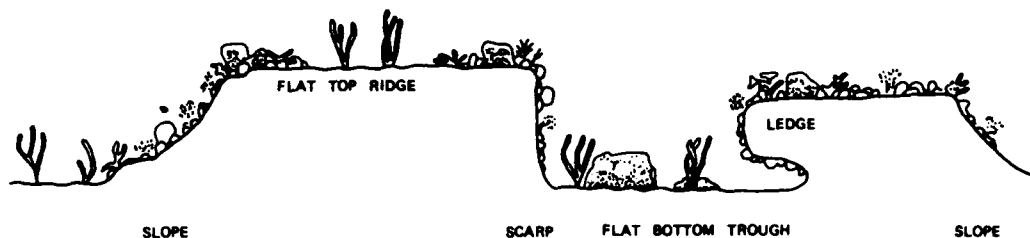

Figure 2-5. Cross section of a representative hard bottom community located 33 km due east of Sapelo Island, Georgia, in 19.8 m of water, and known locally as "Grays Reef" or "Sapelo Live Bottom" (after Hunt 1974)

comprising these hard bottom areas may vary widely in composition according to geographical region and local lithofacies. Hard bottom substrates from the southwest Atlantic have variously been described as recent to subrecent biostromal reef deposits; limestone conglomerates of carbonate shell and quartz sand, stone, sandy biomicrite; and "algal rocks including lithothamnion and coquinalithic deposits" (Menzies et al. 1966; Hunt 1974; Avent, King, and Gore 1977; Continental Shelf Associates 1979; Powles and Barans 1980; U. S. Department of the Interior Bureau of Land Management (BLM) 1978, 1981). Hard bottom habitats are limited to areas where an underlying rock/hard bottom substrate is near the sediment surface, allowing outcropping of exposed rock surfaces in areas where there is sufficient current or wave activity to maintain a sediment-free substrate. Sedimentation is generally not as great a problem as in estuarine environments, but shifting sand from adjacent unconsolidated soft bottoms (storms, currents) may alternately cover up existing low-relief hardbottoms and expose new rock surfaces. The discovery and increasing knowledge of the distributions of hardgrounds or hard bottom habitats have come about in recent years primarily as a

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result of oil exploration activities and fisheries resource investiga-
tions on the continental shelves of the United States (Pearse and
Williams 1951; Menzies et al. 1966; Cerame-Vivas and Gray 1966;
Struhsaker 1969; BLM 1978, 1981; Parker, Colby, and Willis in press).
Hardgrounds have generally been shown to exhibit discontinuous and
patchy distributions, although some northeast-southwest-trending ridges
and troughs have been recently described between Cape Hatteras, North
Carolina, and Cape Canaveral, Florida (Hunt 1974; BLM 1978, 1981).
Three discontinuous hard bottom regions were noted lying parallel to
the coast as follows: inner shelf hardgrounds found in waters between
15 to 27 m deep (Jacksonville, Florida, to Charleston, South Carolina);
middle shelf hardbottoms lying in waters between 28 to 55 m (Jackson-
ville, Florida, to Onslow Bay, North Carolina); and outer shelf banks
(also referred to as "shelf edge reefs") in waters between 55 to 100 m
(Hunt 1974, BLM 1978, Henry et al. 1980). Similar shelfedge features
have been described in the Gulf of Mexico (Bright and Pequegnat 1974;
Bright and Rezak 1976; Bright et al. 1976, 1978a,b; Edwards 1971;
Ludwick and Walton 1957; Parker and Curray 1956). Rock outcrops
observed on the southwest Atlantic shelf may exhibit vertical relief up
to 15 m. Vertical relief is generally 2 m or less within the "inner
shelf hardbottoms," and higher relief rock outcrops are usually re-
stricted to the midshelf and outer shelf environments (Hunt 1974,
Harris 1978, Henry et al. 1980). Hard bottom areas were estimated by
Parker, Colby, and Willis (unpublished manuscript) to cover some
23.3 percent of the shelf between Cape Hatteras and Cape Canaveral,
while those with vertical relief greater than 1 m covered approximately
7.4 percent. Hard bottom habitats with low-relief rock outcrop sur-
faces (less than 0.5 m) may be relatively ephemeral, transient entities
in areas with shifting unstabilized sediments, frequent storm activity,
and strong bottom currents.

39. Marine hard bottom habitats, also known as "live bottoms" and
"reefs," support diverse communities of invertebrates, fish, and algae.
Recent studies have identified 1175 invertebrate species and 150 algae
species from various hard bottom habitats between North Carolina and

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north Florida (Pearse and Williams 1951; Avent, King, and Gore 1977; BLM 1978, 1981). Structurally dominant animal taxa are attached (sessile) to the rock substrate and are predominantly filter/suspension feeders such as sponges, soft coral (alcyonarians), bryozoans, hydrozoans, tunicates, and polychaetes. These taxa serve as substrates or microhabitats for many motile epifaunas and cryptic species (crustaceans, mollusks, echinoderms, polychaetes, etc.). Descriptions of hard bottom communities from North Carolina southward indicate that many of the dominant sessile species and associated taxa common to these habitats are tropical in distribution, whereas adjacent soft bottom benthic communities are not. Many of these tropical species are existing in the northernmost extent of their ranges and are able to do so because of temperature-dampening influences of the Gulf Stream. Compared to adjacent unconsolidated soft bottom communities (Tenore et al. 1978, Hansen et al. 1981) on the southeastern United States continental shelf, hard bottom habitats or live bottom areas are much more productive and support larger populations of virtually every taxa. Fisheries resource investigations on the continental shelf of the southeastern United States have also shown that the live bottom habitats lying between 18 and 55 m are the only habitats in this region capable of supporting commercially exploitable demersal fish stocks (Bearden and McKenzie 1971, Struhsaker 1969, Barans and Burrell 1976, Powles and Barans 1980).

Reef Habitats

Estuarine mollusk reefs

40. Oyster reefs are primarily restricted to estuarine environments although they have been reported in marine coastal environments from North Carolina and the Gulf of Mexico off Louisiana. The eastern or American oyster (*Crassostrea virginica*) is the most widely distributed and commercially important reef-building mollusk species in North America. This species is distributed along the entire east coast of North America, from the Gulf of St. Lawrence, Canada, to Key Biscayne, Florida, to the Yucatan and West Indies (Bahr 1981), and has even been

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reported from Brazil (Gunter 1951). The Pacific oyster (*Oystrea lurida*)
replaces the Atlantic coast species (*C. virginica*) on the west coast,
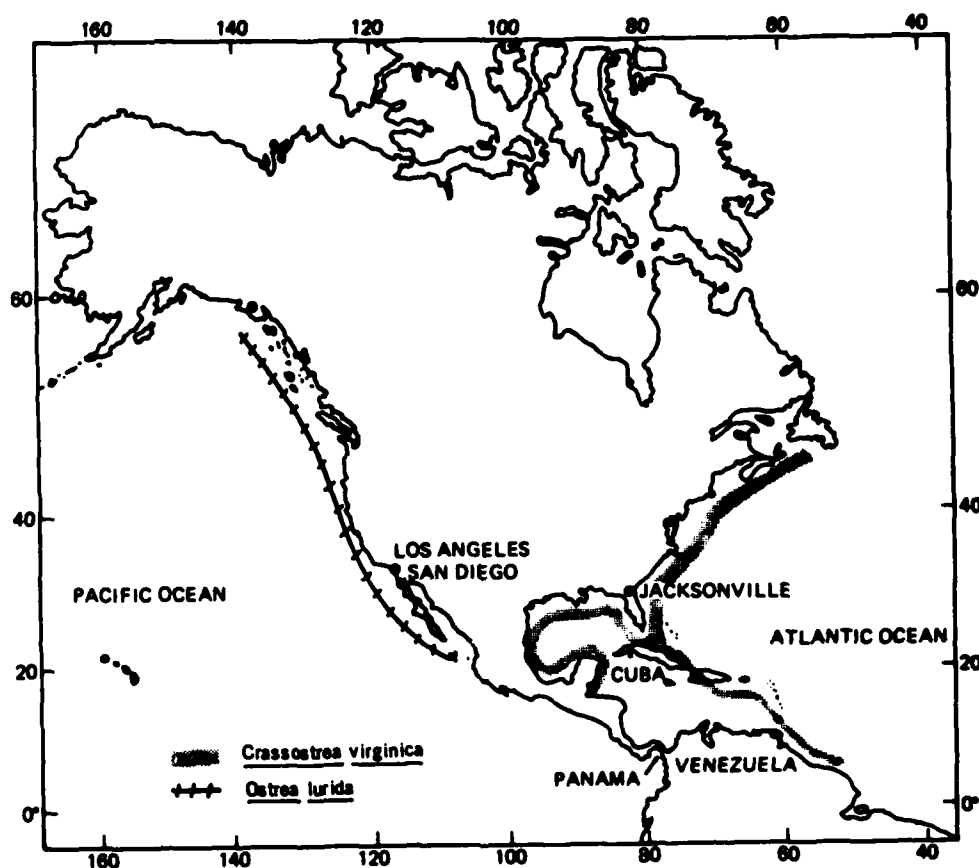and the distributions of both species are shown in Figure 2-6.

Figure 2-6. Oyster distribution patterns in North America
(adapted from Ahmed 1975)

41. Ridge-shaped reefs of the edible oyster, *Crassostrea vir-*
ginica, characteristically develop from shell clusters at favorable
shoreline or nearshore positions, growing out into passing currents and
elongating at right angles to it. Branching or curving of the reef may
occur as the current is deflected by the reef extension (Grave 1901,
1905) (Figure 2-7). Another class of reefs forms along a channel margin
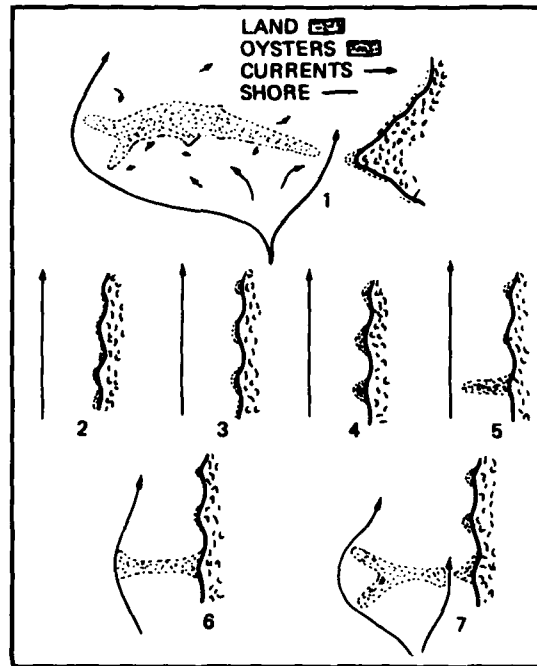
30

Figure 2-7. Oyster reef development in
relation to current/tidal flow direc-
tion in a North Carolina estuary (after
Grave 1901)

and elongates parallel to the dominant currents of the channel. Paired
reefs of this type are common to many inner waterbodies such as central
San Antonio Bay, Texas; Georgia tidal rivers; and the lower James River,
Virginia. The characteristic reefs of most Atlantic estuarine rivers
appear to be elevated ridges on large oval to quadrate oyster beds
(Price 1954). Oyster reefs found along rivers of the Gulf coast are
primarily restricted to their immediate banks (Price 1954).

42. Reefs along the gulf coast have been reported to exhibit a
total shell depth of 18 ft or more, along with several interbedded
layers of mud. Reefs in Texas bays may reach lengths of 1 to 2 miles,
while a few have been reported at 4 to 5 miles in length. The longest
oyster reef complex ever known was reported from Atchafalaya Bay, Loui-
siana, and was some 25 miles in length (Price 1954); this reef is no

longer viable due to altered hydrologic conditions from Mississippi River Channel diversion. Oysters have a wide distribution in estuaries from seawater (35 ^{o}/oo) to oligohaline (3 ^{o}/oo) zones and are found in a wide range of depths, with many reefs particularly well developed in the intertidal zone. They generally exhibit higher growth rates in higher salinity waters. Their distributions within estuaries are largely limited by predator pressure and diseases. Most predators are relatively stenohaline. Major oyster predators, such as the gastropods *Thais* spp. and *Urosalpinx* spp., have a lower salinity tolerance of 8 and 10 ^{o}/oo, respectively (Gunter, Ballard, and Venkataramiah 1974). Other significant predators such as the stone crab *(Menippe mercenaria)*, the boring clam *(Martesia)*, and the boring sponge *(Cliona celata)* are also distributed primarily in the higher salinity areas (Gunter, Ballard, and Venkataramiah 1974). Periods of high salinity coupled with high temperatures may result in mass mortality from the protozoan, *Perkinsus marinus* (Mackin 1951, Overstreet 1978). An oyster pathogen severely infecting oysters in the lower Chesapeake Bay and Delaware Bay is the sporozoan *Minchinia nelsoni* (or MSX). This disease causes high mortalities and has sharply reduced the size and distribution of oyster beds in the affected areas, although this pathogen also appears to have a lower salinity tolerance of 15 ^{o}/oo.

43. Oysters provide a large substrate and habitat for epifaunal community associates. Bahr (1974) estimated that a minimum of 50 m^2 of surface area was available for epifaunal habitation for every square meter of reef area. Studies of oyster reefs have shown them to be faunally diverse communities (Figure 2-8). Wells (1961) has described some 303 invertebrate species associated with oyster reef habitats in the Newport River estuary, North Carolina.

44. The blue mussel, *Mytilus edulis*, may also form enormous reefs, especially at northern latitudes, where it hangs on the rocky substrates.

Coral reefs

45. Carbonate coral reef environments represent one of the most structurally complex and faunally and floristically diverse and

Figure 2-8. Oyster Community (after Hedgepeth 1953)

productive ecosystems on earth (Figure 2-9). Odum and Odum (1955), in
a comprehensive study of the coral reef structure and function of a
windward Pacific reef community, found the mean annual standing crop
biomass of primary producers to be 703 g/m^2/year; herbivores, 132 g/m^2/
year; and carnivores, 11 g/m^2/year. The primary production rate of
the coral reef community was estimated at 8760 g/m^2/year (production-to-
biomass (P/B) ratio = 12.5), although the net production is relatively
low due to the high metabolic requirements (production-to-respiration
ratio (P/R) = 1) of the community. Sessile benthos which are the struc-
tural, dominant species in coral reef communities are primarily auto-
trophic, and there are relatively few heterotrophic plankton feeders
other than coral polyps (Odum and Odum 1955). Stony corals (Scleractina
and Hydrozoa) are major contributors to the calcium carbonate reef de-
posits, although calcareous red algae (lithothamnia) may be of equal or
greater importance, especially on the seaward side of the reef, where

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4 mm (approximate scale)

Figure 2-9. Marine invertebrates inhabiting a coralline stone, illustrating the diversity of animals in coral reef habitats (from INVERTEBRATE ZOOLOGY by Robert D. Barnes. Copyright (c) 1980 by Saunders College/Holt, Rinehart and Winston. Copyright (c) 1963, 1968, 1974 by W. B. Saunders Company. Reprinted by permission of Holt, Rinehart and Winston, CBS College Publishing)

they are better able to tolerate the pounding surf (Odum 1971). It has
been suggested (Odum 1971) that perhaps coral reefs could be more cor-
rectly referred to as "coral-algal reefs." The intimate association of
the animal coral polyp with its symbiotic plant associate (Zooxanthel-
lae) living within enables hermatypic (corals with symbiotic Zooxanthel-
lae) or reef building corals to be essentially self-sustaining ecosys-
tems (Johannes et al. 1970; Franzisket 1964; and Goreau, Goreau, and
Goreau 1979). Reef-building corals (hermatypic) are found on the south-
eastern shores of the Americas, typically from Miami, Florida, south-
west to the Dry Tortugas; the Caribbean Island, including Puerto Rico
and the Virgin Islands; and the Pacific Islands, including Hawaii.
Coral reef habitats are less common off the western shores of the Amer-
icas, and California and western Mexico have no extensive reef forma-
tions due to generally cooler waters. A few westward extensions of the
West Indian reef system have been described from provinces or "salt
domes near the shelf break" (Hedgepeth 1954, Bright et al. 1976) sea-
ward of Texas and Louisiana in the northern Gulf of Mexico, known as
the "Flower Garden Banks." To date some 253 invertebrate species and
103 fish have been described from this peculiar reef system. Reefs off
Florida support an extremely diverse community of invertebrates, fish,
and algae.

46. Coral reef habitat are stenotopic, delicately balanced eco-
systems. Dominant coral reef species generally require stable tempera-
tures, uniform salinities, and clear water, and surrounding waters us-
ually exhibit low nutrient levels. Temperature ranges are critical for
reef-building corals, and coral reefs are only found within a range of
$16°$ to $36°$ C (Smith 1971). Optimum growth occur within a narrow tem-
perature range of $23°$ to $25°$ C. The observed critical salinity range
for reef corals is 24 to 40 $°/oo$, although reefs are generally found in
oceanic salinities of 35 $°/oo$. Corals may be exposed to temporary
salinity reductions and physical abrasion after tropical storms and
hurricanes. Reef-forming corals are generally restricted to depths of
90 m or less (Smith 1971; Goreau, Goreau, and Goreau 1979), and vigorous
growth is generally limited to within 30 m of the surface. These corals

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require high light intensities to support and maintain the symbiotic Zooxanthellae. Moreover, the fouling of reefs with sediment is particularly harmful to the delicate organisms making up the coral community, as their ability to remove sediment deposited on them is quite limited (Grigg 1970; Goreau, Goreau, and Goreau 1979). For this reason, and because of intolerances to salinity and temperature stresses, they are not as well developed in embayments and nearshore on the western Atlantic and gulf coasts. Reefs are generally located on the windward side of shorelines. The reefs of Florida and Hawaii are usually described as fringing reefs, although they differ somewhat from this definition. Florida's reefs are more aptly named bank reefs, built upon a shallow sea platform which was once the bottom of a shallow sea covering the southeastern portion of the United States (Smith 1971).

Worm reefs

47. Worm reefs are formed by massive colonies of polychaetes in the family Sabellariidae, which have a wide distribution on both east

A. FEEDING POSITION
B. WITHDRAWN INTO TUBE

Figure 2-10. Semischematic diagram of *Phragmatopoma lapidosa* Kingberg (after Kirtley and Tanner 1968)

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and west coasts as well as the Gulf of Mexico (Figure 2-10). However, reef forming sabellarids are generally more commonly found in subtropical to tropical waters along the Atlantic Coast and the Gulf of Mexico, including the Virgin Islands and Puerto Rico. A sabellariid worm reef has also been reported from Delaware Bay (Wells 1970, Curtis 1978), although the polychaete forming this reef, *Sabellaria vulgaris*, does not form reefs throughout most of its geographical range, except off the north Florida Atlantic Coast (Figure 2-11). Reefs are constructed by large colonies of sabellariid worms living within individual tubes constructed of cemented sand grains. When found in estuaries they are generally restricted to higher salinity areas near the mouth, with sufficient current or wave activity and suitable sized particles for tube building. Scattered worm reefs reported from Baffin Bay, Texas, are of interest due to the high salinities of up to 80 ^{o}/oo reported from this hypersaline estuary (Hedgpeth 1954). Worm reefs are recognized as being an effective protection against beach erosion. Sabellariid reefs are known to occur between lat. 72° N and 53° S, and their widespread distribution indicates their stability potential along modern coastlines. The distribution of sabellariid reefs along the Florida coast are indicated by Figure 2-11. Because these animals depend on water turbulence for tube-building materials, food, and removal of metabolic wastes, the size and shape of the reefs is dependent upon prevailing local wave energy levels and water mass circulation properties (Kirtley and Tanner 1968). Littoral sabellariid reefs are found in belts of 100 m or more in width, lying parallel to the shoreline in elongated bands which are often cut by numerous surge channels; or they are found as rounded mounds (Figure 2-12). They are commonly found in depths of up to 5-10 m, although most are confined to depths of several meters (Multer and Milliman 1967). These reefs generally do not support as rich and diverse a fauna as do coral or mollusk (oyster/mussel) reefs.
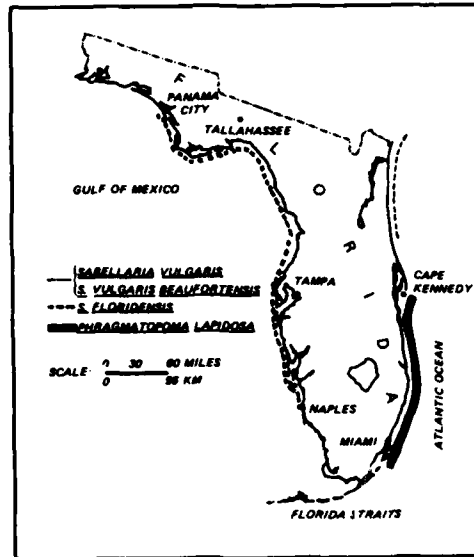
Figure 2-11.   Distribution of
sabellariid worm reefs along
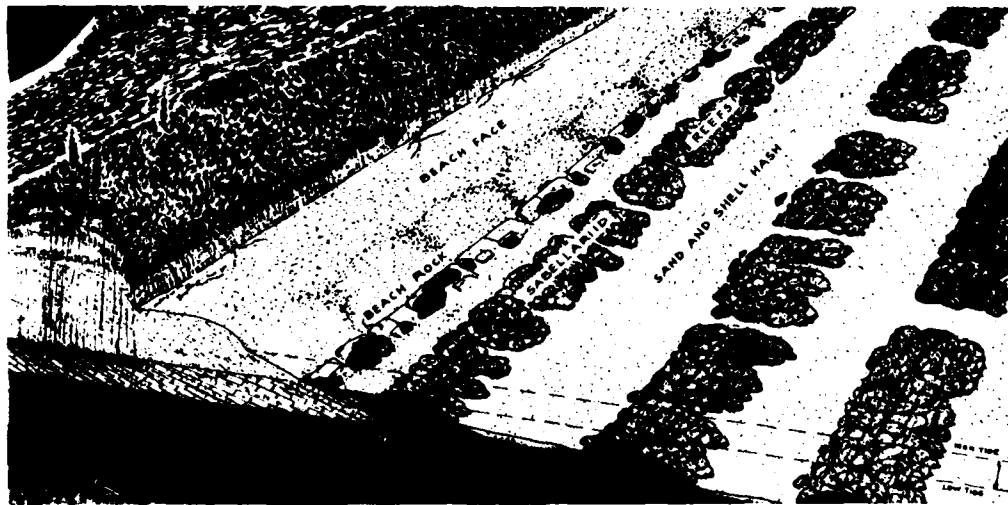the Florida coast (after
    Kirtley and Tanner 1968)

Figure 2-12.   Schematic drawing showing the shape and distribution of
            sabellariid reefs (after Kirtley 1966)

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PART III

HABITAT DESCRIPTORS

48. The following chapter discusses the important measurable habitant parameters structuring estuarine and marine benthic habitat types in terms of their potential influence on the composition, density, and secondary production of benthic macroinvertebrates. Because of their importance, water quality descriptors such as salinity and temperature will be discussed separately in this report. Other water quality parameters, such as dissolved oxygen, turbidity, and general pollution, will be discussed in paragraphs 71 through 81 under the heading Water Quality. The important habitat descriptors in the estuarine and marine system are: (a) salinity, (b) substrate quality, (c) vegetation quality, (d) temperature, (e) current velocity, (f) depth, and (g) water quality.

Salinity

49. The significance of a water quality factor such as salinity in structuring benthic communities diminishes in coastal marine environments, while it is of major importance in estuarine environments. Salinity is regarded as a major factor delimiting the distributions of organisms along the axis of an estuary in every habitat class from freshwater to open-ocean salinities (Gunter, Ballard, and Venkataramiah 1974). Estuaries may be classified as homeohaline or poikilohaline, based on the relative magnitude of salinity fluctuations over a tidal cycle or between seasons at any given location within an estuary from limnetic (freshwater) to euhaline (seawater) zones. The rate and frequency of change of salinity . turn, dramatically affects the observed distribution of species along the salinity gradient (halocline), based on an individual species ability to tolerate the range of salinities encountered (Figure 3-1). Benthic faunas have been classified into ecological categories based on their observed distribution patterns in estuaries (Day 1967, Carriker 1967,
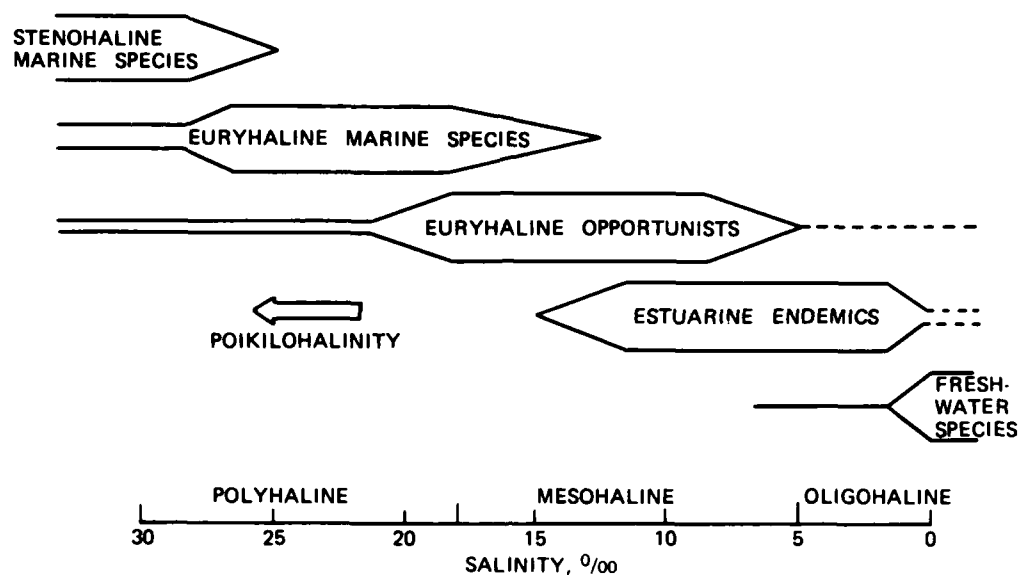

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Figure 3-1. Schematic of the faunal and floral distributional
classes along the halocline of a homeohaline estuary (after
Boesch 1977b)

Boesch 1977b). These categories are as follows:

a. Stenohaline marine. Marine species largely restricted
to waters of high, relatively stable salinities near the
mouth of the estuary.

b. Euryhaline marine. Marine species exhibiting fairly
broad salinity tolerances and distributions throughout
an estuary.

c. Euryhaline opportunistic. Marine species capable of ex-
ploiting environments where environmental stress is
high (variable salinity, temperature, dissolved oxygen)
and biotic interaction is generally low. This group is
usually more abundant in salinities of 10-20 ^{o}/oo, or in
shallow habitats subject to frequent disturbance.

d. Estuarine endemic. Organisms evolved from marine forms,
but now restricted to estuaries and never found in the
sea.

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e. __Freshwater.__ Comprised of a few salt-tolerant examples of freshwater species derived from rivers, and restricted to low-salinity areas (upper reaches) of estuaries.

f. __Migratory.__ A variety of actively motile species (portunid crabs, shrimp, etc.), which move in and out of an estuary on feeding and spawning migrations.

50. In homeohaline estuaries, the salinity fluctuations are relatively stable and well defined over time, occurring around the boundaries of the "Venice Classification System," as depicted in Figure 3-1. Biotic distribution discontinuities or zones of more abrupt biotic change generally coincide within salinity limits of 30, 18, 5, and 0.5 ^{o}/oo for homeohaline estuaries. Therefore, faunal changes along the salinity gradient within homeohaline estuaries are gradual and relatively uniform along the axis of the salinity gradient, with a well-defined zonation of species from stenohaline marine to limnetic. A study by Boesch (1977b) of the Chesapeake Bay, a homeohaline estuary, showed a gradual and relatively constant change in macrobenthic species abundance along the salinity gradient, with somewhat accelerated changes occurring within the 20-15 ^{o}/oo range and in the 8-3 ^{o}/oo range, coinciding very closely with the Venice system.

51. The initial Classification scheme proposed by Carriker (1967) based on the "Venice System" for relatively homeohaline estuaries, has been modified by Boesch (1977b) to also include poikilohaline-type estuaries (Figure 3-1). In tidally and seasonally poikilohaline estuaries, the rate of change and magnitude of salinity fluctuations occurring within a reach or entire estuary do not fit into the classic "Venice System" salinity ranges. The degree of poikilohalinity, or rate and magnitude of salinity change, limit the distribution of stenohaline species (marine and freshwater). Lower limits of salinity tolerance delimit the distribution of faunas along the salinity gradient, and estuarine endemic and euryhaline opportunistic species will generally exhibit a much wider range of distribution in tidally and seasonally poikilohaline estuaries compared with homeohaline estuaries. For this reason the Venice Classification System as originally proposed

(Carriker 1967) is inappropriate for poikilohaline-type estuaries, and Boesch's (1977b) scheme is more appropriate. The terms poikilohaline and homeohaline may also be used to describe portions of an estuary based on the observed range of salinity changes over time for any given reach of an estuary. Faunal distribution patterns for any given location or reach of an estuary are generally limited by tidally and seasonally minimum salinity conditions rather than by average salinities (Boesch 1977b).

52. Salinity has also been shown to affect the infaunal and epifaunal components of the benthic fauna somewhat differently, as substrate (unconsolidated sediments) may moderate the short-term fluctuations in salinity. This causes the sediment interstitial salinity environment of the infauna to fluctuate less than the water column salinity environment of the epifauna (Sanders, Mangelsdorf, and Hampson 1965). These two benthic faunal components are recognized as being ecologically distinct (Thorson 1957).

53. Marine coastal environments on the other hand exhibit a much smaller range of salinity fluctuation compared to estuarine environments. Salinity fluctuations are closely linked by proximities to major river mouths (Emery and Uchupi 1972). Figure 3-2 shows the average monthly salinity and temperature fluctuations for seven coastal shelf stations. Small-scale changes in salinity are generally a response to seasonal river discharge rates, precipitation (storm) cycles, and temperature-regulated evapotransportation. Changes in salinity are relatively small and decrease with increasing distance from river mouths as influences of river runoff diminish. Figure 3-3 shows the latitudinal salinity distribution and its relationship to precipitation minus evaporation. Figure 3-4 depicts the vertical (depth) and monthly distribution of salinity for five areas on the northwestern Atlantic shelf. It shows that salinities are generally much more stable near the bottom relative to the surface and usually vary little more than 1 ^{o}/oo over an annual cycle. Therefore, salinities encountered in marine coastal environments may only be critical to benthic habitats during exceptionally severe storms such as hurricanes, or in nearshore
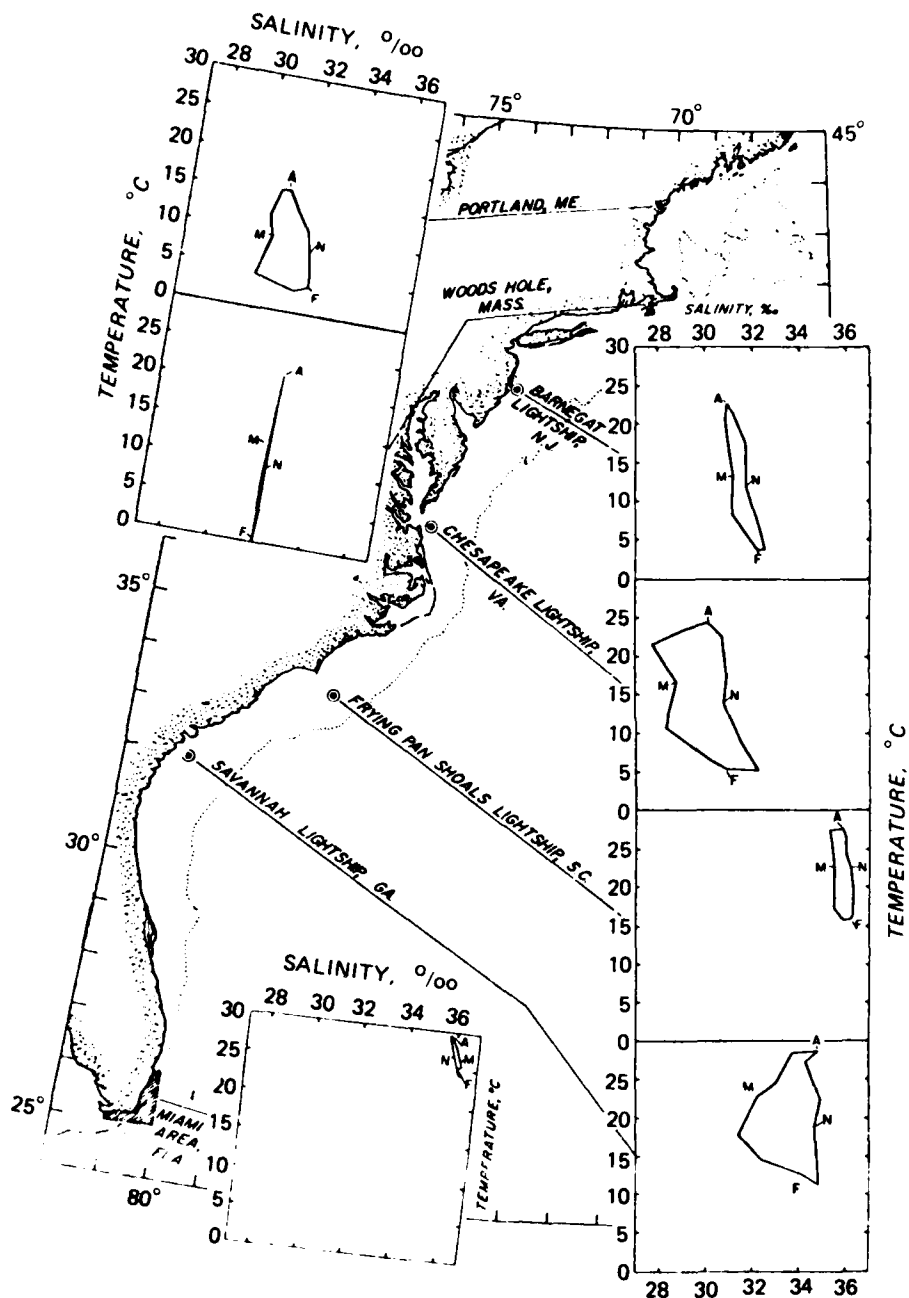
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Figure 3-2. Polygons showing average salinities and temperatures at seven hydrographic stations in the northwestern Atlantic; M = May, A = August, N = November, and F = February (after Emery and Uchupi 1972)
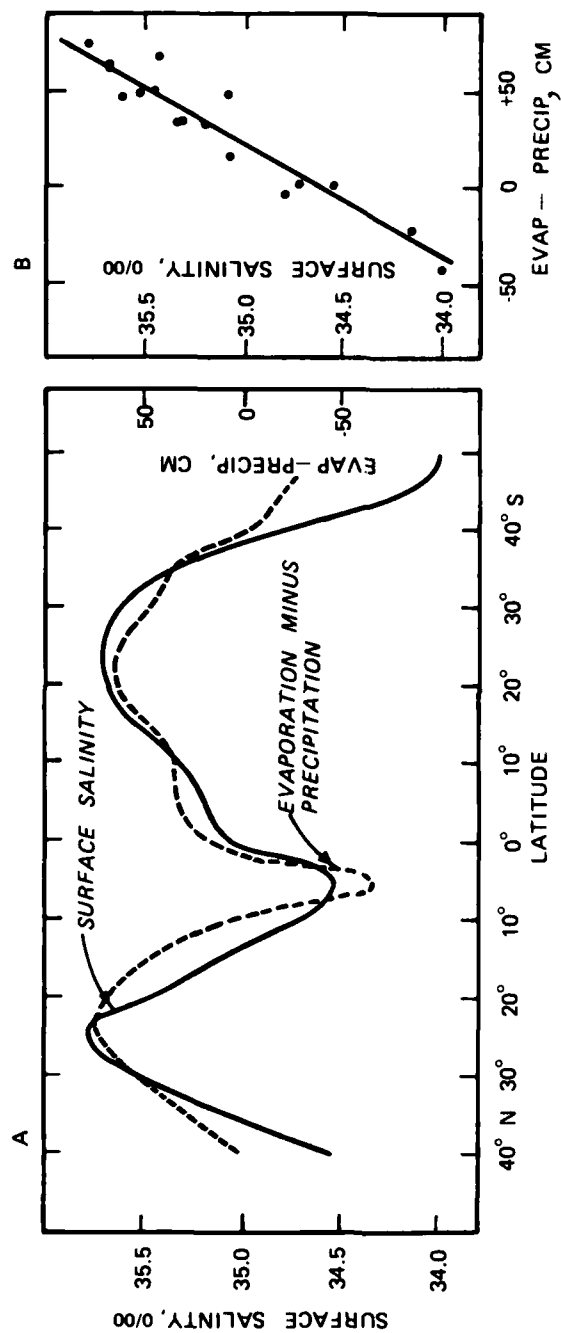
Figure 3-3. (A) Plots of (1) average surface salinity for all oceans and (2) the difference between evaporation minus precipitation, plotted against latitude. (B) A plot of the relationship between surface salinity and the difference between evaporation minus precipitation (after Sverdrup, Johnson, and Fleming 1942)
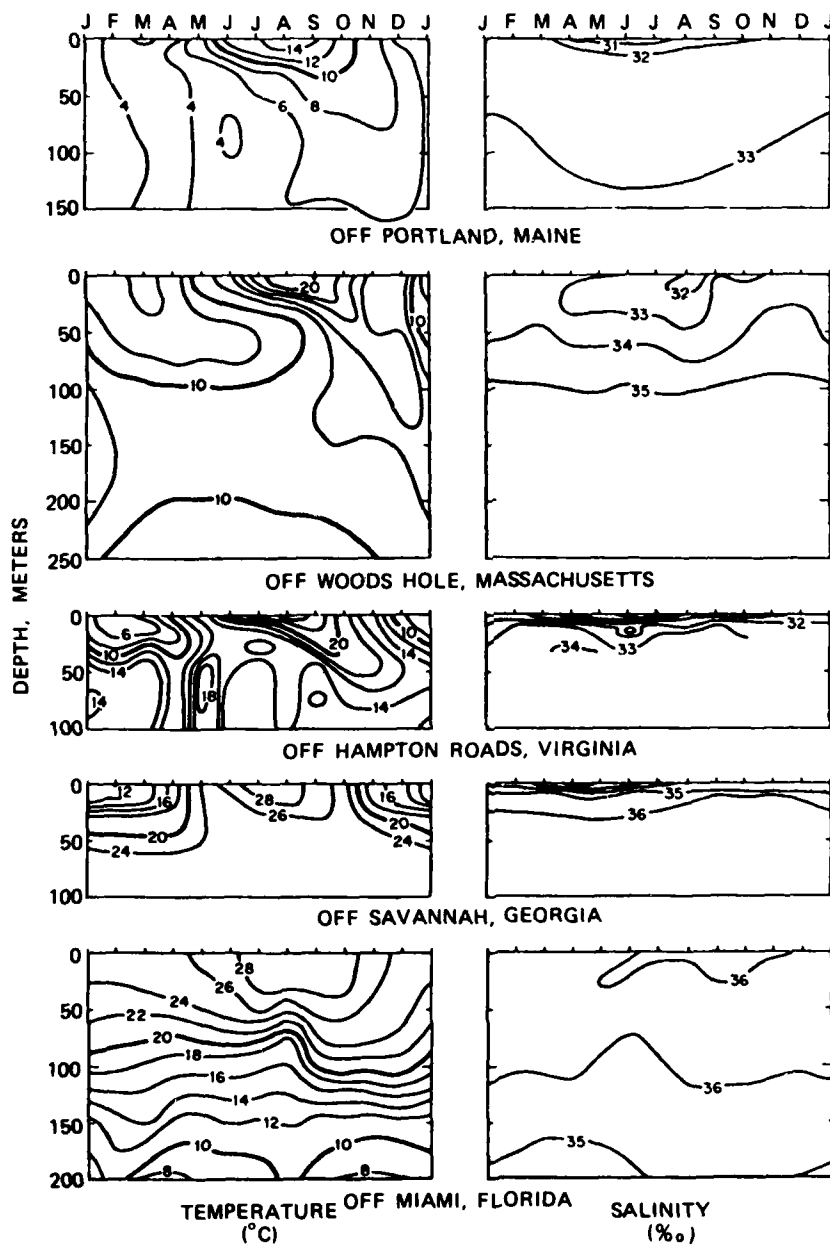
Figure 3-4. Vertical (depth) temperature (°C) and salinity (°/oo) profiles over time showing the seasonal/depth shifts in temperature and salinity from five areas on the northwestern Atlantic continental shelf (hydrographic stations depicted on map in Figure 3-2) (after Emery and Uchupi 1972)

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areas subject to river mouth influences, or in areas affected by major currents like the Gulf Loop current.

54. The following discussion will summarize the effects of salinity within each estuarine benthic habitat type.

a. <u>Unconsolidated soft bottom habitats.</u> Soft bottom communities are comprised of infaunal and epifaunal species. Sediments moderate or dampen short-term salinity fluctuations caused by tidal circulation or meteorological events, thereby creating a more hospitable environment for infaunal communities during short-term oscillations in salinity in overlying waters. Sediment interstitial salinities are in turn dependent to a large extent on grain-size composition (clay, silt, sand) because sediment porosity markedly influences the diffusion rate of water into and out of the sediments. Epifaunas living on the surface of unconsolidated soft bottom habitats are subjected to the full range of salinity fluctuations during a tidal cycle or storm event, and are more likely to encounter unfavorable salinities, especially in poikilohaline reaches of estuaries (Sanders, Mangelsdorf, and Hampson 1965; Burbanck and Burbanck 1967). This would explain the relatively impoverished epifaunas in mesohaline (5-18 $^{\circ}$/oo) and oligohaline (0.5-5.0 $^{\circ}$/oo) environments where salinity fluctuations are highest. In poikilohaline estuarine systems, the number of epifaunal species generally drops at a faster rate along the gradient of increasing salinity fluctuations, compared to infaunal species (Sanders, Mangelsdorf, and Hampson 1965). Nevertheless, the richness of total infaunal and epifaunal species decreases markedly along the salinity gradient from high to low salinity. Figure 3-5 illustrates the observed species richness, faunal density, and magnitude of tidal salinity change along the axis of a Georgia river estuary within sand bottom habitats. Figure 3-6 illustrates a similar gradient of species richness for individual taxa as a function of salinity along the axis of a tidally poikilohaline estuary. Stenohaline marine taxa such as echinoderms and bryozoans are quickly extinguished from the fauna, while all taxa show decreased species richness as salinity decreases. The obvious trend is one of decreasing species richness with increasing poikilohalinity and decreasing salinity. Similar faunal gradients of decreasing species in the mesohaline zone relative to the polyhaline zone have also been found in soft bottom habitats of the homeohaline Chesapeake Bay System (Boesch 1972, Nilsen et al. unpublished). Apparent observations of decreased total faunal abundances in the
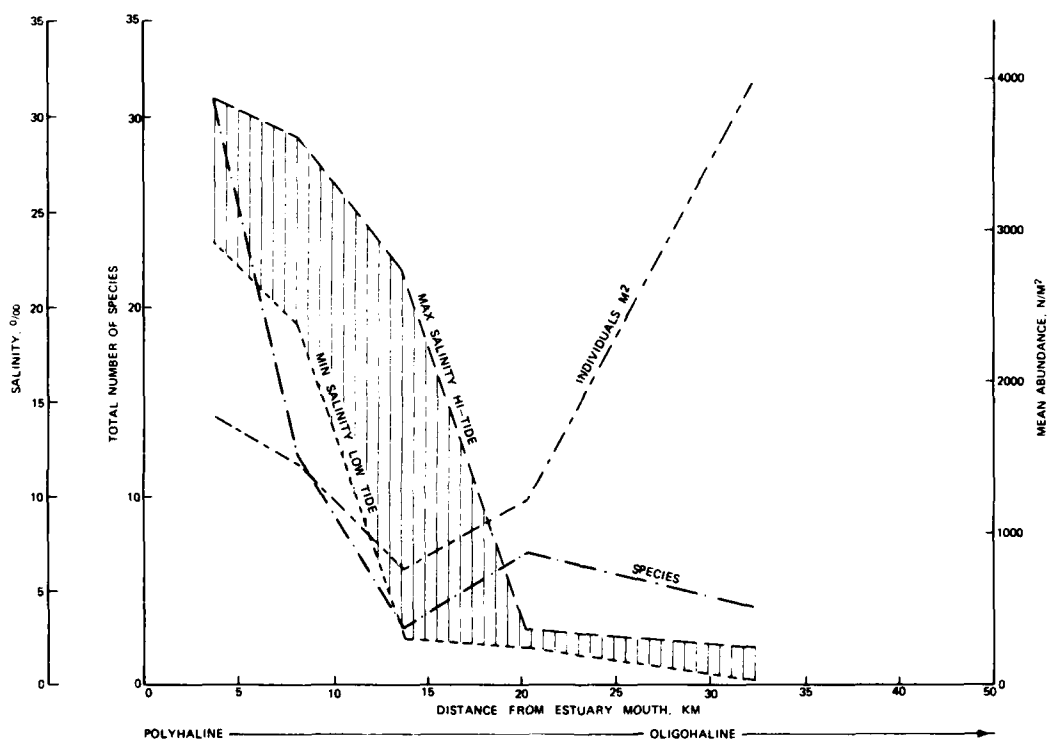
Figure 3-5. Macrobenthos distribution patterns in sand habitats
(point bars) in the Ogeechee River Estuary, Georgia, along a
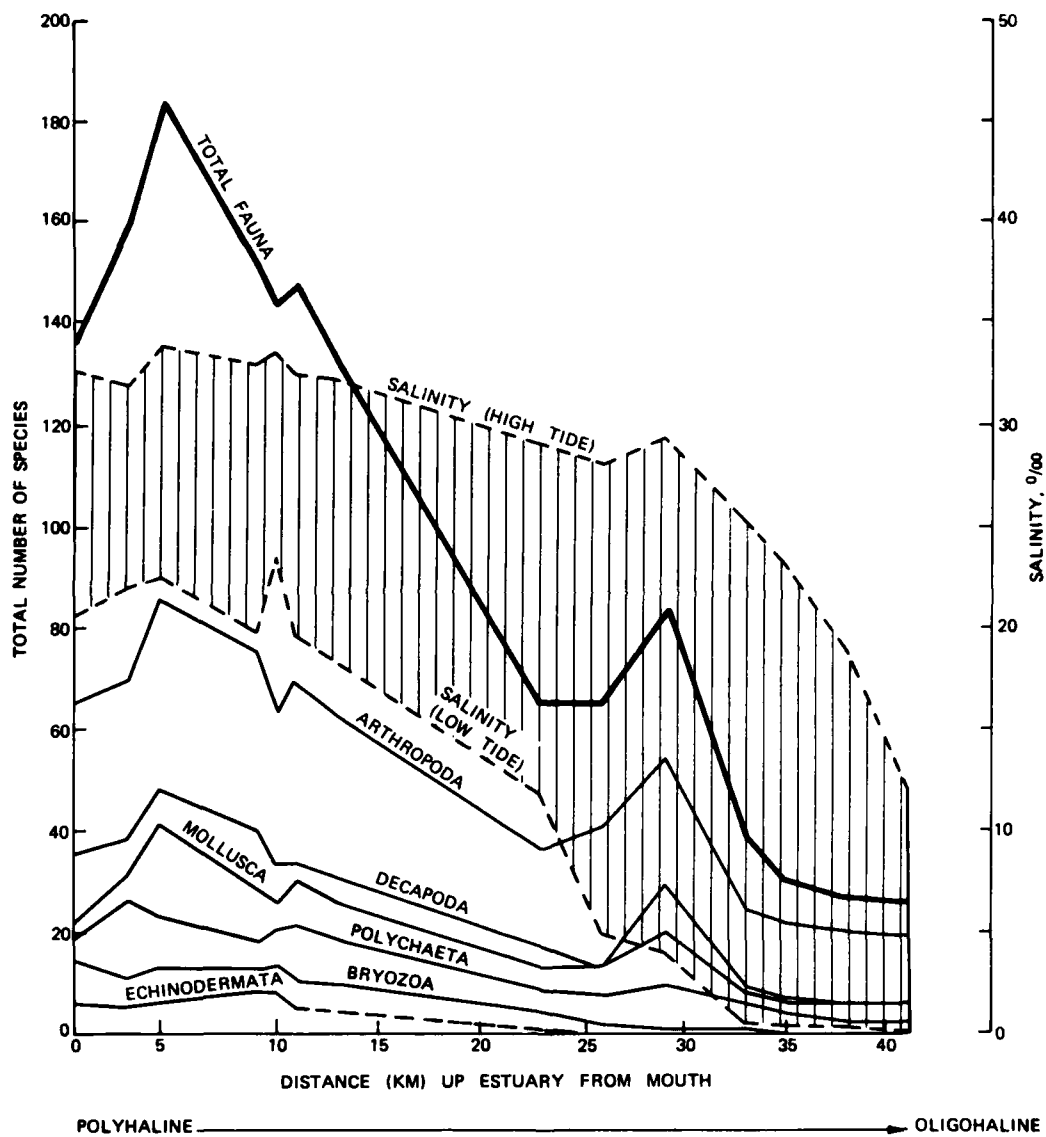halocline (after Howard, Elders, and Heinbokel 1975)

Figure 3-6. Macrobenthic invertebrate distribution along
a salinity gradient in a poikilohaline estuary, Georgia
(data from Howard and Frey 1975)

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mesohaline zone depicted in Figure 3-5 may be an arti-
fact of that particular study (Howard, Elders, and
Heinbokel 1975) rather than a generally observed corre-
lation; as other studies have shown no such trend
(Boesch 1972, Kendall 1974,*).

<u>b</u>. <u>Submerged aquatic vegetation habitats.</u> The discussion
of submerged aquatic vegetation habitats (paragraphs 28-
32) showed that salinity was an important factor in de-
limiting the habitat boundaries of each vegetation type.
Macrobenthos associated with vegetated habitats are in
turn influenced by fluctuations in salinity along the
axis of a habitat. Only a few studies have addressed the
impact of variable salinity on macrobenthic communities
from vegetated habitats. Figure 3-7 illustrates one
such study for seagrass *Halodule wrightii* in the sub-
tropical Indian River estuary, Florida (Young and Young
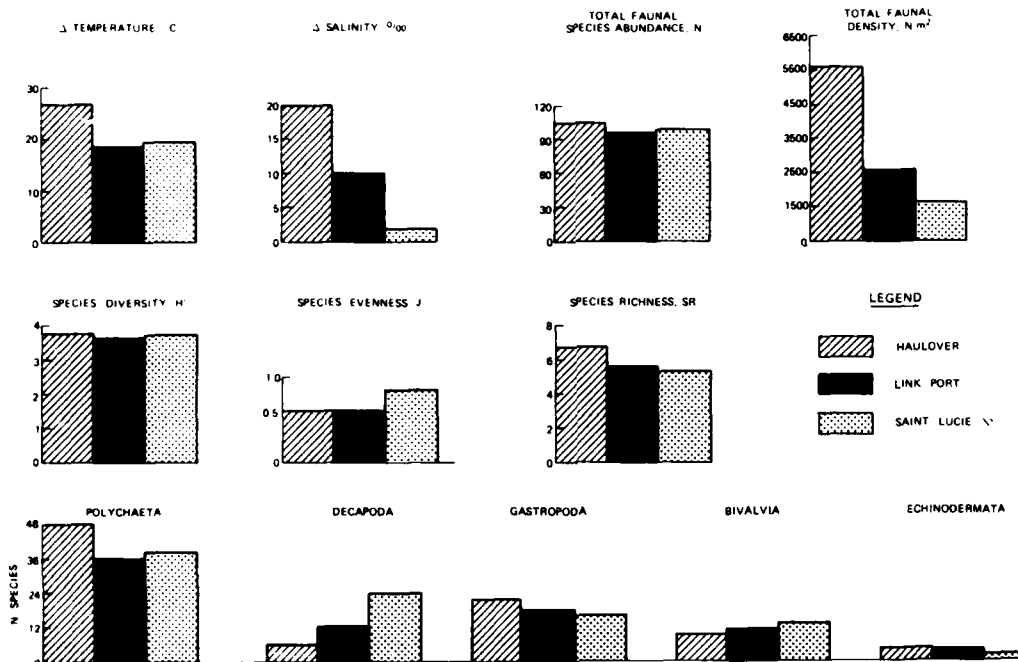
Figure 3-7. Effects of environmental stress (salinity and
temperature) on uncaged areas of subtropical seagrass bed
macrobenthic communities (data from Young and Young 1977).
Note: see Pielou (1966a) for the equation used to derive
species diversity (H'), Margalef (1958) for the equation
for species richness (SR), and Pielou (1966b) for the
equation for species evenness (J')

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* Personal Communication, 1981, D. F. Boesch, Director, Louisiana
Universities Marine Consortium, Chauvin, La.

1977). This study showed that in the seagrass habitat stressed by variable salinity and temperature, the number of species and the values of indices for species diversity, evenness, and richness did not vary significantly from those of the more environmentally stable habitat; the structure of the community changed, however, favoring high densities of eurytopic opportunistic species at the environmentally stressed site (see Table 2-1). Note the subtle changes in the faunal composition at the three seagrass habitat sites, showing increased numbers of polychaete and gastropod species at the stressed site, while decapods and and bivalves showed decreased numbers of species with increasing salinity and temperature stress. A study of eelgrass (*Zostera*) faunal species richness and abundance along an environmental gradient of fluctuating salinity and temperature by Orth (1973) showed decreased numbers of benthic infaunal species and generally decreased densities in lower salinity eelgrass habitats than in higher salinity habitats (Table 3-1). Subtle differences noted between the subtropical seagrass and temperate seagrass habitats from these two examples suggest caution should be exercised when attempting to extrapolate observed benthic community responses to environmental stresses (salinity and temperature) among similar types of seagrass habitats separated by large latitudinal ranges. Salinity-related impacts on community structure in seagrass habitats have been described by Orth (1974). He found lowered salinity levels following Tropical Storm Agnes (1972) caused marked reductions in faunal community structure in eelgrass beds.

Table 3-1
Benthic Infaunas of *Zostera* Beds in the Chesapeake Bay-York River

Estuary (Seasonal Distributions at Four Stations with

Different Salinities (after Orth 1973))

Station	Salinity Range,* (^{o}/oo)	Species (N) Spring	Summer	Density (N/m^2) Spring	Summer
A	19-24	62	55	32,913	14,725
B	18-23	56	50	24,333	21,000
C	16.5-22.5	48	42	8,696	11,899
D	12-20	25	31	11,304	4,754

* Estimated from figure in Orth (1973).

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c. __Reef habitat.__ Oyster reef habitats are widely distributed within estuaries between 35 and 3 ^{o}/oo, although the most productive reefs are generally found in the mesohaline (5-18 ^{o}/oo) to polyhaline zones (18-30 ^{o}/oo) (Galstoff 1964). In some estuaries, such as Chesapeake Bay and Delaware Bay, outbreaks of oyster diseases (MSX, *Perkinsus*) and large predator populations may limit the oyster producing areas to salinities below 15 ^{o}/oo. The distribution of benthos associated with oyster reefs clearly responds to salinity changes along the halocline of an estuary. A classic illustration of salinity effects on epifaunas and infaunas of oyster communities is shown in Figure 3-8 for the Newport River estuary in North Carolina (Wells 1961). Species abundance drops off sharply from euhaline to polyhaline/mesohaline environments. Freshets in the upper reaches of estuaries (<10 ^{o}/oo) resulting from storms and/or abnormally high river inflows may cause high mortalities in oyster populations. A 6-week period of low-salinity water in the James River, Virginia, caused oyster mortalities approaching 90 percent in some oyster beds (Andrews 1973). Figure 3-9 shows a similar period of low-salinity water observed by Wells (1961) in the Newport River estuary after the passage of three hurricanes. This period of freshened water caused high mortalities in oyster community associates. Lowered salinity associated with large storm events may indirectly benefit oyster communities by temporarily ridding oyster reefs of stenohaline predators such as starfish and oyster drills (Wells 1961, Andrews 1973).

d. __Rock/hard bottom habitat.__ Epifaunas associated with estuarine rock/hard bottom habitats are generally similar in structure to those found in typical oyster reef communities, and a similar reduction in species abundance along the halocline of an estuary would be expected. Species recruitment to hard bottom habitats would also reflect the magnitude of the environmental stress. Figure 3-10 shows fouling community recruitment along an environmental stress gradient of increasing salinity and temperature fluctuations in a subtropical Florida estuary. The study shows a sharp reduction in fouling epifaunal species with decreasing salinities and increasing fluctuations in temperature and salinity (Mook 1980).

51
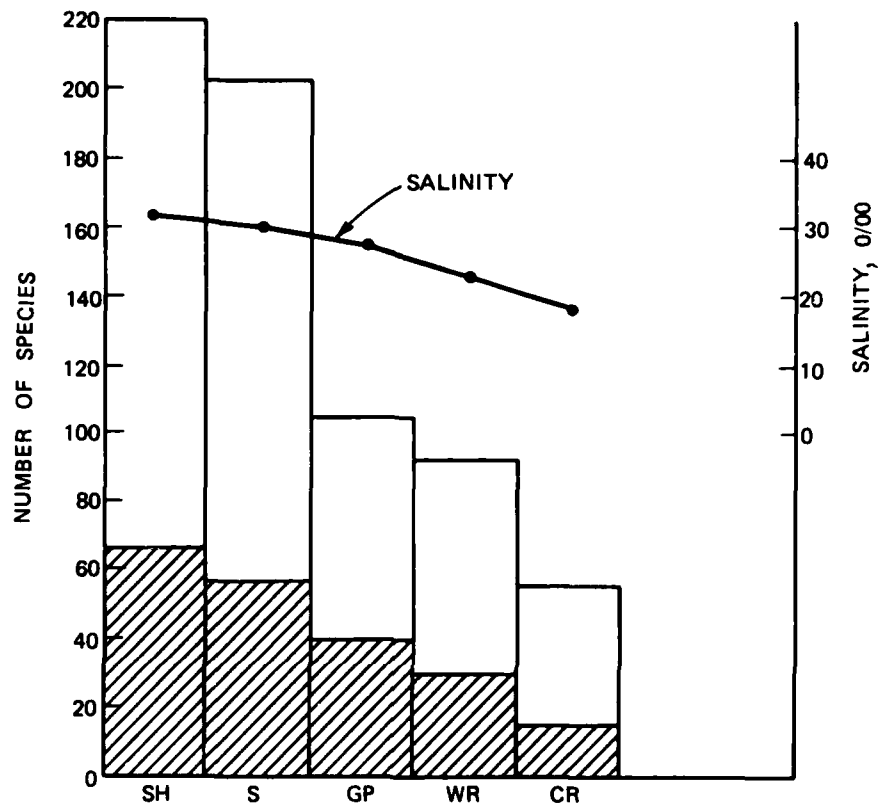
LEGEND

SH   SHARK SHOAL

S   SLUICEWAY

GP   GALLANT POINT

WR   WHITE ROCK

CR   CROSS ROCK

▨   MEAN NUMBER OF SPECIES

☐   TOTAL NUMBER OF SPECIES

Figure 3-8. Cumulative total and mean number of invertebrate species collected per sampling interval (monthly) and mean salinity for each oyster reef station in Newport River estuary, North Caroline (after Wells 1961)

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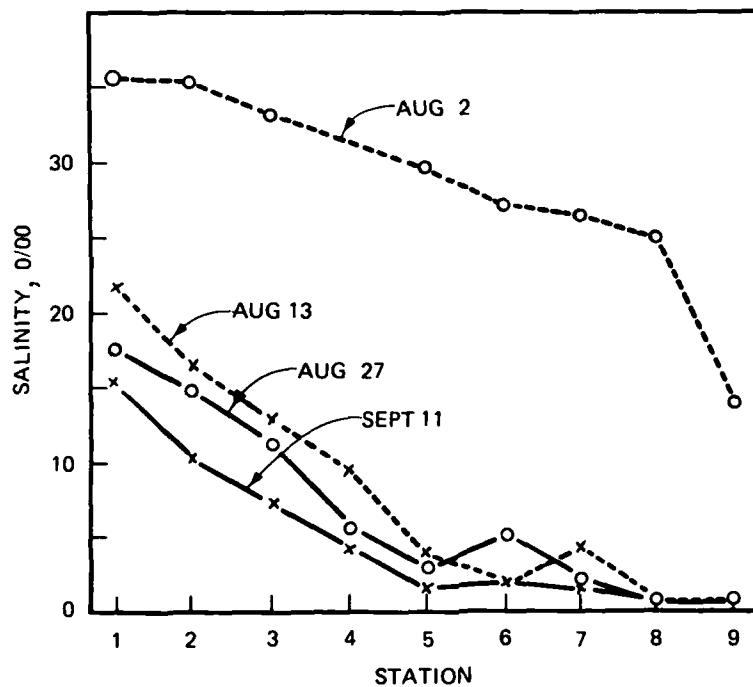Figure 3-9. Salinity profiles from Newport River estuary, 1955. Hurricane Connie passed through on August 12, and Hurricane Diane on August 17 (after Wells 1961)

LEGEND

FP = FT. PIERCE INLET
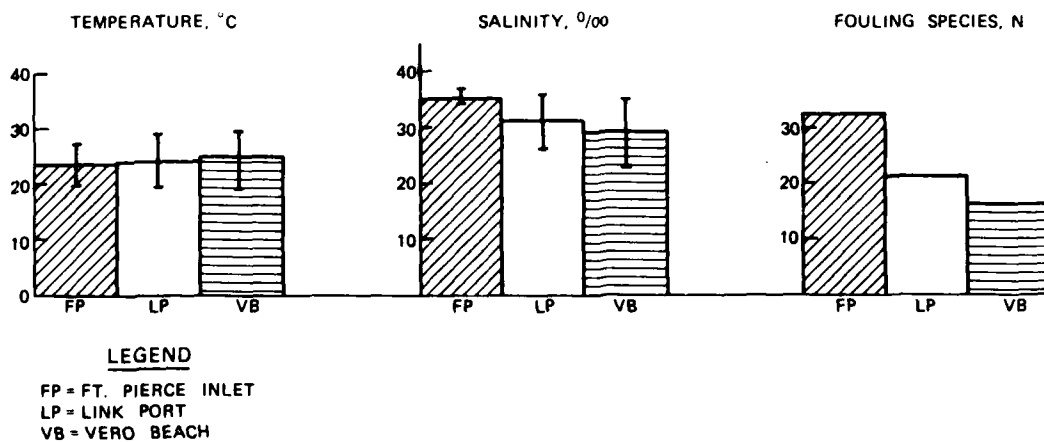LP = LINK PORT
VB = VERO BEACH

Figure 3-10. Fouling community settlement along an environmental stress gradient. Temperature and salinity are expressed as averages with ranges depicted (data from Mook 1980)

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Substrate Quality

55. Substrate quality parameters such as percent organic carbon, grain size distribution, sediment depth, shear strength, etc., are major factors influencing the distribution of marine benthic organisms (Peterson 1913; Jones 1950; Thorson 1955, 1957; Hedgepeth 1953) and have been demonstrated to be important factors for estuarine organisms as well (Sanders 1956, 1958, 1960; Rhoads and Young 1970; Young and Rhoads 1971; Wells 1957; Pratt 1953; Bloom, Simon, and Hunter 1972; McNulty, Work, and Moore 1962; Johnson 1970, 1972; Boesch 1973; Burbanck 1981). Although Muus (1967) has concluded that dominant estuarine benthic species are to a large extent eurytopic with respect to sediment type, many species and trophic groups show clear sediment affinities. Substrate composition and stability in unconsolidated and consolidated sediments will affect the types of benthos found on any particular bottom type. Substrates are vital as a source of attachment and as a food source for associated benthos. Sessile epifaunal benthos require consolidated, firm substrates for attachment. Burrowing, suspension feeding, and tube building infaunas modify the quality and may enhance the stability of unconsolidated sediments by binding inorganic and organic particles together as fecal pellets and pseudofeces, by the redistribution of sediments by feeding activities or tube building, and by the secretion of mucopolysaccharides (Fager 1964; Rhoads 1963, 1974). Benthic infauna may influence sediment stability and subsequent erodibility by reworking the near-surface sediment layers and increasing porosity due to subsurface burrowing activities (Biggs 1967; Rhoads 1974; Rhoads, Yingst, and Ulman 1978; Yingst and Rhoads 1978). The following discussion will illustrate the relationships between substrate and benthos within each habitat type.

  a. Unconsolidated soft bottom. Important sediment properties of soft bottom estuarine and marine sediments are particle size distribution, organic content and quality, and stability (shear strength). An important property of a sediment is its particle size distribution, which is a description or characterization of the sediment by discrete particle size classes as shown by the

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Wentworth Grade Classification based on geometric class
intervals (Table 3-2). A note of caution is in order
concerning the mechanical analysis of sediments. Meth-
ods most frequently used are based on techniques bor-
rowed from soil science that do not consider biological
modifications of sediments following biogenic reworkings
by deposit feeding and suspension feeding benthos (Rhoads
1974; Johnson 1974, 1977). Benthos may completely modify
the physical characteristics of the sediment by binding
silt and clay size particles into aggregate particles
that behave as sand-size particles (McCall 1979, Leving-
ton 1977). Mechanical analyses of sediments destroy
these aggregate particles and change the composition of
the sediment to uniform unaggregated particles which may
have little ecological meaning (Buchanan and Kain 1971;
Morgan 1956; Rhoads 1974; Johnson 1974, 1977).

(1) Sediments have been broken down into major qualita-
tive (i.e., according to organic matter, carbon,
calcium carbonate, and inorganic matter content)
and particle size classes based on subjective and
objective analyses. Pratt (1953) and Wells (1957)
analyzed animal-sediment relationships in two
estuaries based only on subjective visual/textural
classification of sediments. Both found significant
animal-sediment relationships using this approach
(Figures 3-11 and 2-3). Objectively, particle size
fractions of sediment may be classified into a sedi-
ment type using a classification scheme similar to
Shepard (1954), whereby the three major size class
fractions (clay, silt, sand) are plotted on a tri-
angular graph, as shown in Figure 3-12.

(2) The significance and quality of organic matter to
organisms living in sediments cannot be ignored as
it is utilized chiefly as food by deposit feeding
benthos (Tenore 1975, 1977). Davis (1925), among
others, felt that the association of various groups
of animals with soils of particular textures is not
so much influenced by the texture per se as by the
food conditions of which the size of the soil
particles is a correlated indication. Sanders
(1956, 1958) suggested clay was the most valid
sediment correlate for the distribution of deposit
feeding organisms living on organic matter in or
on fine-grained sediments (muds). Clays are much
smaller than silt-size particles and therefore
have a much larger surface area to bind organic
matter serving as a primary source of food for
deposit feeding benthos. Sanders (1956) found the
largest populations of benthos in Long Island

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Table 3-2

Sediment Classification Schemes

Sediment Particle Size Classification (after USEPA 1973)		
Name	Particle Size mm	U. S. Standard Sieve Series No.
Boulder	>256	--
Rubble	64-256	--
Coarse gravel	32-64	--
Medium gravel	8-32	*
Fine gravel	2-8	10
Coarse sand	0.5-2	35
Medium sand	0.25-0.5	60
Fine sand	0.125-0.25	120
Very fine sand	0.0625-0.125	230
Silt	0.0039-0.0625	400
Clay	<0.0039	Evaporate and weigh residue

Sediment Classification Using the Wentworth Scale** with 2, $\sqrt{2}$, and ϕ
Notation (After Buchanan and Kain 1971)

	2 scale mm	$\sqrt{2}$ scale mm	ϕ
	2	2	-1
		1.41	-0.5
	1	1	0
		0.71	+0.5
Sand	0.50	0.50	+1.0
		0.351	+1.5
	0.250	0.250	+2.0
		0.177	+2.5
	0.125	0.125	+3.0
		0.088	+3.5
	0.062	0.062	+4.0
		0.044	+4.5
	0.031	0.031	+5.0
		0.022	+5.5
Silt	0.0156	0.0156	+6.0
		0.0110	+6.5
	0.0078	0.0078	+7.0
		0.0055	+7.5
	0.0039	0.0039	+8.0
Clay	{<0.0039	<0.0039	

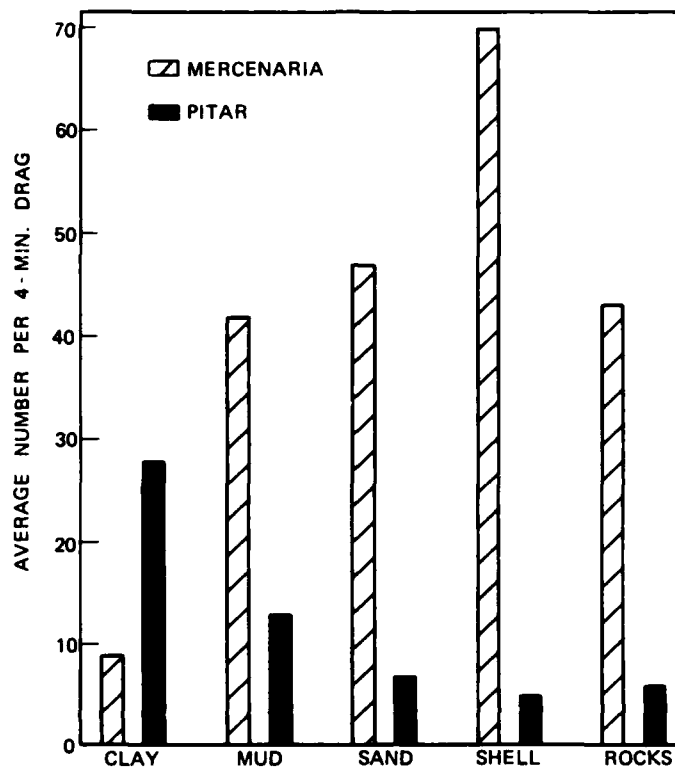* Standard sieves with 8- to 16-mm mesh are available.
** Wentworth 1922.

Figure 3-11. Abundance of two bivalve species as a
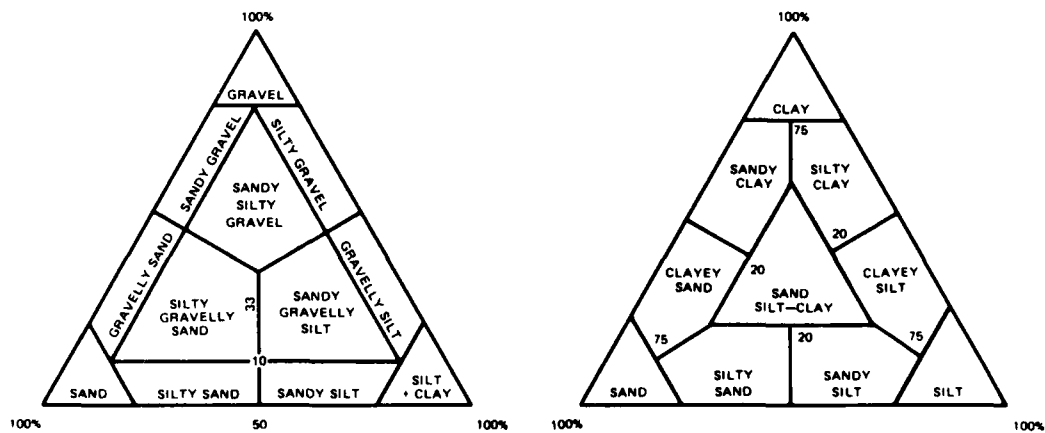function of sediment type (after Pratt 1953)

Figure 3-12. Triangular graphic methods of presenting
data (after Buchanan and Kain 1971)

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Sound in sediments with 13-25 percent silt and clay. Burbanck (1981) found higher dominance and lower species diversity and biomass in fine-grained sites than coarse-grained sediments in Delaware Bay. In carbonate sediments, clay may not be a good indicator of deposit feeding abundance, as illustrated by a recent study by Santos and Simon (1974). They compared deposit feeding polychaete distributions from carbonate sand bottoms in two seagrass and three unvegetated sand habitats in a subtropical Florida estuary and found no relationship between deposit feeding abundances and silt-clay content. Silt-clay levels were very low, 0.0-1.0 percent, although very high deposit feeding (polychaete) densities were found (averaging 13,525/m^2), three times those observed by Sanders in his study of Long Island Sound (4,430/m^2). The high densities observed by Santos and Simon may have occurred because seagrass proximities to unvegetated sites provided a detrital food source (Figure 3-13). Levington (1977) attributed lower deposit feeding abundances in an unvegetated muddy-sand habitat in a Massachusetts estuary to resource (food) limitations. In estuarine unconsolidated soft bottom habitats, more or less optimum mixtures of clays, silts, fine sands, and organic matter support greater densities of macrobenthos than either clean coarse unstable sands and gravels at the mouths of estuaries or soft slurry muds in the quiet sheltered reaches of estuaries (Carriker 1967).
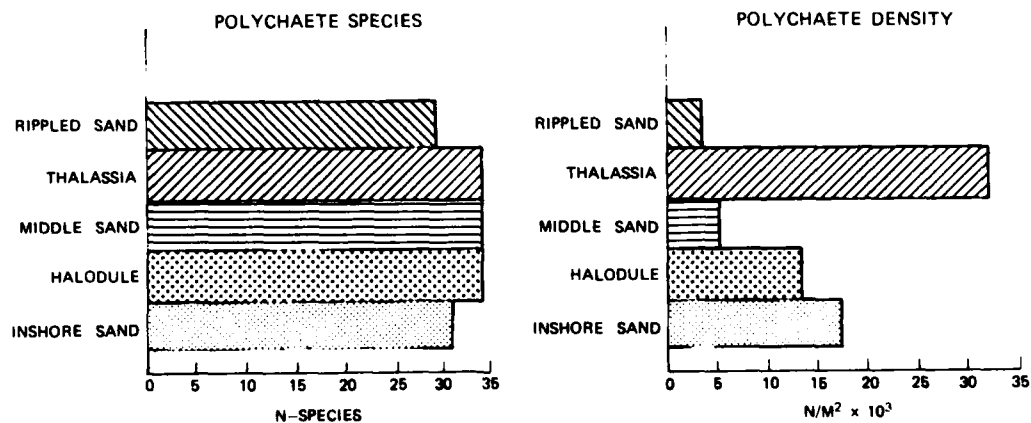

Figure 3-13. Interhabitat comparisons of infaunal polychaete structure (data from Santos and Simon 1974)

(3) Extensive sampling of coastal marine shelf sediment
environments from Nova Scotia to Mexico depicted in
Table 3-3 gives some indication of qualitative
changes in sediment encountered along a latitudinal
gradient. Perhaps the most noticeable change found
is in the relative amount of calcium carbonate ma-
terial. The amount of biogenic calcium carbonate
increases dramatically at lower latitudes near Key
West, Florida, where it makes up an average of
55 percent of the sediments. Large rivers such as
the Mississippi River make substantial contribu-
tions to shelf sediments as shown by Table 3-3,
while sand makes up only 10 percent of the sedi-
ments in this region, the finer grain sizes com-
prising the bulk of the sedimentary material.

(a) East, gulf, and west coast marine soft bottom
textural gradients suggest there is a general
increase in silt-clay and organic contents
with increasing distance (depth) offshore, and
a corresponding increase in sediment stability
(Boone, Granat, and Farrell 1978; Emery and
Uchupi 1972; Flint and Holland 1980). Sub-
strate texture changes were closely linked
with macrobenthic community structure changes
in a transect study of benthic communities on
the southern California continental shelf by
Barnard and Hartman (1959). They identified
three sediment texture/depth zones: sand
(42-72 ft), silty-sand (90-150 ft), and mud
(180-360 ft). Highest macrobenthic standing
crops were found in the silty-sand habitats

with mean biomass estimates of 1370 g/m^2 (wet
weight); decreasing shoreward and seaward in
the other two substrate types, due to benthic
community structure changes. However, textural
gradients may vary substantially due to local
sediment sources, currents, and bathymetry.
Observed quantitative distributions of macro-
benthos from different sediment types indicate
that sediment quality does influence the stand-
ing crop of benthos, but that the relationships
are complex and contradictory in some in-
stances. Table 3-4 shows the observed stand-
ing crop biomass averages for nine sediment
types ranging from gravel to clay within three
latitudinal ranges. It can readily be seen
that the observed distributions of benthos
standing crop were not uniform with latitude
or sediment type. Moreover, silty-sand

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Table 3-3

Average Properties of Shelf Sediments: Nova Scotia to Mexico

(after Emery and Uchupi 1972)

	Nova Scotia to New York	New York to Cape Romain	Cape Romain to Key West	Key West to Mississippi River	Mississippi River to Mexico
Physical Composition, percent					
Sand	65.0	100.0	100.0	91.0	10.0
Silt	2.0	0.0	0.0	0.0	0.0
Clay (<4µ)	1.0	0.0	0.0	0.0	0.0
Silty clayey sand	5.0	0.0	0.0	3.0	26.0
Clayey sandy silt	5.0	0.0	0.0	6.0	13.0
Sandy silty clay	8.0	0.0	0.0	0.0	25.0
Sand-silt-clay	14.0	0.0	0.0	0.0	26.0
Chemical Composition					
Calcium carbonate, percent	1.8	2.5	17.8	55.0	6.3
Organic carbon, percent	0.49	0.19	0.16	0.25	0.53
Kjeldahl nitrogen, percent	0.097	0.023	0.030	0.037	0.070
Carbon/nitrogen ratio	5.0	8.1	5.2	6.9	7.5

Table 3-4

Standing Crop* of Benthic Animals, Nova Scotia to Key West (g/m^2)

(after Emery and Uchupi 1972)

Sediment Type	Nova Scotia to New York	New York to Cape Romain	Cape Romain to Key West
Gravel	277	n.d.**	n.d.
Sand-gravel	131	21	n.d.
Glacial till	82	n.d.	n.d.
Shell	192	574	203
Sand-shell	81	78	70
Sand	208	81	79
Silty sand	237	771	27
Silt	164	82	n.d.
Clay	194	n.d.	n.d.

* Based upon about 1400 samples from depths between 0 and 200 m.
** Not determined, mainly because of inadequate number of samples.

substrates showed both the highest benthic standing crop (771 g/m^2) between New York and Cape Romain, South Carolina, and the lowest (27 g/m^2) between Cape Romain and Key West. This makes quantitative and qualitative generalizations about any given sediment type difficult to make because other environmental factors besides grain size distributions are also likely to influence the benthos distributions and densities within any given sediment type. Broadly speaking, the distributions and densities of benthos become more stable from nearshore to deepwater environments, primarily as a response to increased environmental stability (Sanders 1968, 1969; Flint and Holland 1980). Sediment quality changes also occur, which may affect the benthos composition. For example, Jumars and Fauchald (1977) found relative increases in numbers of sessile polychaete species with increasing depths up to 400 m along a depth transect on the Pacific Coast, which were attributed to increasing

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sediment stability. Observed spatial/depth sediment textural changes (i.e., increasing sediment stability, silt-clay content, organic content) on the Oregon shelf (mouth of the Columbia River) were also related to benthic faunal changes in biomass, density, and species diversity and richness, all increasing off-shore (Boone, Granat, and Farrell 1978). Frankenberg and Leiper (1977) found high seasonal and spatial variability in nearshore littoral benthic communities on the Georgia shelf. Sediments in these relatively shallow (3.5- to 21-m) shelf environments are subject to frequent disturbances such as storms and greater climatic variability. Therefore, communities dominating these environments may reflect the "opportunistic life history 'strategies'" discussed by McCall (1977, 1978) (see Table 2-1). A study by Buchanan, Sheader, and Kingston (1978) found macrobenthos species diversity negatively correlated with silt content, although not with depth. They found biomass negatively correlated with depth, but not with sediment type.

(4) A highly successful method for objectively analyzing and classifying complex animal-sediment relationships and species associations is the use of numerical classification procedures such as cluster analysis, ordination, and discriminant analysis (Clifford and Stephenson 1975, Boesch 1977a, Shin 1982). Boesch (1973) was able to identify habitat and species groups using numerical classification procedures for the macrobenthos in the Chesapeake Bay region (homeohaline estuary), and found sediment factors such as clay, silt, and the availability of hard substrates overwhelmingly responsible for the observed spatial patterns in benthos. He found epifaunas poorly developed on mud bottoms with high silt contents, relative to sand bottoms with more suitable substrates (i.e. shell). In general, he observed much higher diversities of infaunas and epifaunas on sand bottoms relative to mud bottoms, as shown in Table 3-5. Higher diversities frequently observed in sand bottoms may be a consequence of microhabitat complexity (e.g. variable grain sizes) (Sanders 1968, Boesch et al. in review).

(5) In stressed (e.g. poikilohaline) estuaries animal-sediment relationships may not be as clearly

Table 3-5

Soft Bottom Habitat Comparisons; Homeohaline Estuary

(data from Boesch, 1973)*

Habitats	Species Abundance	Density N/m²	Species Diversity (H')	Species Richness (SR)	Species Evenness (J')	Number Stations
Mud	23 ± 9	2525 ± 2756	2.3 ± 0.9	3.8 ± 1.4	0.52 ± 0.19	6
	(9-29)	(520-7780)	(0.8-3.4)	(1.7-5.7)	(0.19-0.71)	
Mud/Sand	40 ± 8	1403 ± 687	4.0 ± 0.5	7.0 ± 1.1	0.75 ± 0.09	9
	(31-55)	(735-2860)	(3.2-4.8)	(5.5-8.9)	(0.64-0.86)	
Sand	49 ± 11	3045 ± 1736	4.0 ± 0.5	7.7 ± 1.4	0.72 ± 0.08	24
	(33-65)	(730-8865)	(2.9-4.9)	(5.3-11.5)	(0.57-0.84)	

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* Mean ± standard deviation (SD) (range of values observed at all stations).

defined due to overriding environmental stress
factors (Dörjes and Howard 1975; see habitat type
description, paragraph 19). In these systems, the
source of the stress, e.g. salinity, current veloc-
ity, etc., may be more suitable for identifying
faunal spatial distribution patterns using classi-
fication procedures. The multispecies structure
of biological data may be explored and simplified
using either of two different multivariate models.
Each is capable of elucidating biological patterns
that can be used in subsequent analyses of rela-
tionships with abiotic variables. In the case of
large, spatially heterogeneous data sets, discrete
(classification) models seem most tractable. When
single gradients predominate (e.g., a stress gra-
dient such as salinity, current, etc.), continuous
models (ordination and discriminant analysis and
correlation) tend to be more useful in data inter-
pretation. Numerical classification techniques have
also been used to identify benthic assemblages in
coastal marine shelf environments in relation to
sediment type, depth, environmental change, and
current or water movements. Attempts to relate the
benthic fauna distribution in terms of substrate
particle size have usually failed to find sharp
animal-sediment relationships using classification
techniques on the South Atlantic and Northern Gulf
of Mexico continental shelf (Day, Field, and Mont-
gomery 1971; Flint and Holland 1980); this tool,
however, has been successful in classifying benthos
animal-sediment relationships in the Middle At-
lantic Bight.* Most investigations have generally
found benthic faunal associations more closely
related to depth than sediment textural changes,
although some definite textural/faunal trends are
apparent (Day, Field, and Montgomery 1971; Boesch
1973; Boone, Granat, and Farrell 1978; Flint and
Holland 1980; Jumars and Fauchald 1977). Attempts
at classifying animal-sediment relationships may
be unsuccessful when sediment characterization
studies are incomplete. Sediment characterizations
based on simplistic measurements of only gross
sediment composition (i.e., percent clay, silt,
sand, organic content) may not be sufficient to
distinguish subtle animal-sediment relationships,
especially in shelf environments; in these environ-
ments sand particle size composition, for example,

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* Personal Communication, 1981, D. F. Boesch, Director, Louisiana
Universities Marine Consortium, Chauvin, La.

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may exhibit large variations within-habitat (i.e., according to where the particles occur on the crest or trough of a sand wave). It has been suggested (Boesch et al. in review) that these subtle variations in particle size distribution within a sand habitat may explain the large variations in species composition and abundance often observed in shelf environments.

b. Aquatic vegetation bed. Substrate qualities are significant to and will affect the distribution of either submerged vascular plants and/or algae attached to the bottom. Seagrass species living in soft bottom environments generally require a reducing sediment environment, although the actual composition of sediments may be wide ranging. Both eelgrass and turtle grass require a strongly reduced sediment layer to become established (Phillips 1978, 1980; Zieman 1975). The Pacific surf grasses *Phyllospadix* spp, on the other hand, require a rock/hard substrate for attachment, as do the kelp bed communities found along the northwest Atlantic and Pacific Coasts. A delicate chemical equilibrium exists in sediments characteristic of seagrass beds, where strongly reducing conditions prevail below a 1-cm depth (Phillips 1978, 1980; Young and Young 1977; Zieman 1975). The oxidation of this strongly reduced layer from physical disruption of the sediments may render the sediments unsuitable for future growth of seagrasses. This was observed in a *Zostera* bed following eelgrass denuding by feeding swans (Wood 1959) and following destruction of eelgrass beds by cownose rays (Orth 1975). For high production, turtle grass beds appear to require reducing conditions in the sediments surrounding the rhizomes and roots (Phillips 1960). Substrate composition within and outside seagrass beds may vary from one location to another, and caution should be exercised when inferring substrate conditions from one seagrass habitat to another. The following example will illustrate the different sediment compositions observed within *Thalassia testudinum* beds from Bermuda and Florida, as a function of plant density. Figure 3-14 illustrates the sediment particle size, plant biomass, and faunal species richness and densities for a Florida turtle grass system. It shows no significant differences in sediment composition and faunal densities as plant densities increased (except faunal densities were much lower at the lowest plant density station) (Stoner 1980). There was also an apparent decrease in faunal biomass with increasing plant cover at the higher plant density stations (Stoner 1980). A study by Santos and Simon (1974) in another Florida estuary also found no sediment compositional
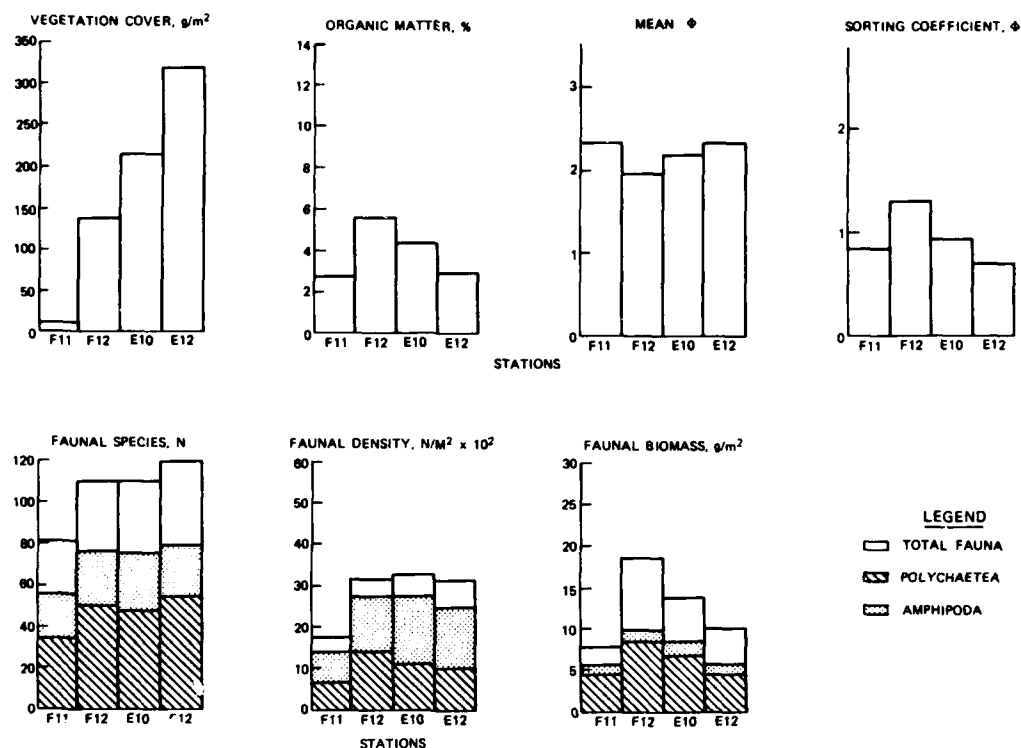
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Figure 3-14. The role of seagrass biomass *(Thalassia)* in structuring
macrobenthic assemblages (data from Stoner 1980)

differences between sand, *Thalassia*, and *Halodule* habi-
tats, with mean grain sizes approximating those observed
by Stoner (1980). However, Orth (1977a) *found signif-
icant differences across the seagrass bed for* both
Thalassia in Bermuda and *Zostera* in Chesapeake Bay for
sediment particle size and for organic matter and plant
biomass (Figures 3-15 and 3-16). Clay and silt-size
particles increased as plant biomass increased. These
sedimentological differences were also correlated with
increased faunal abundances in the finer grained sedi-
ments, but vegetation biomass was also a covariable.
Figure 3-17 contrasts the large differences in faunal
diversity and abundance observed between a *Thalassia*
seagrass bed and an adjacent unvegetated sand habitat
(Orth 1977a).

(1) Seagrass species have been found glowing in a wide
variety of sediment compositions from mud to coarse
sand. Eelgrass has been reported growing in a wide
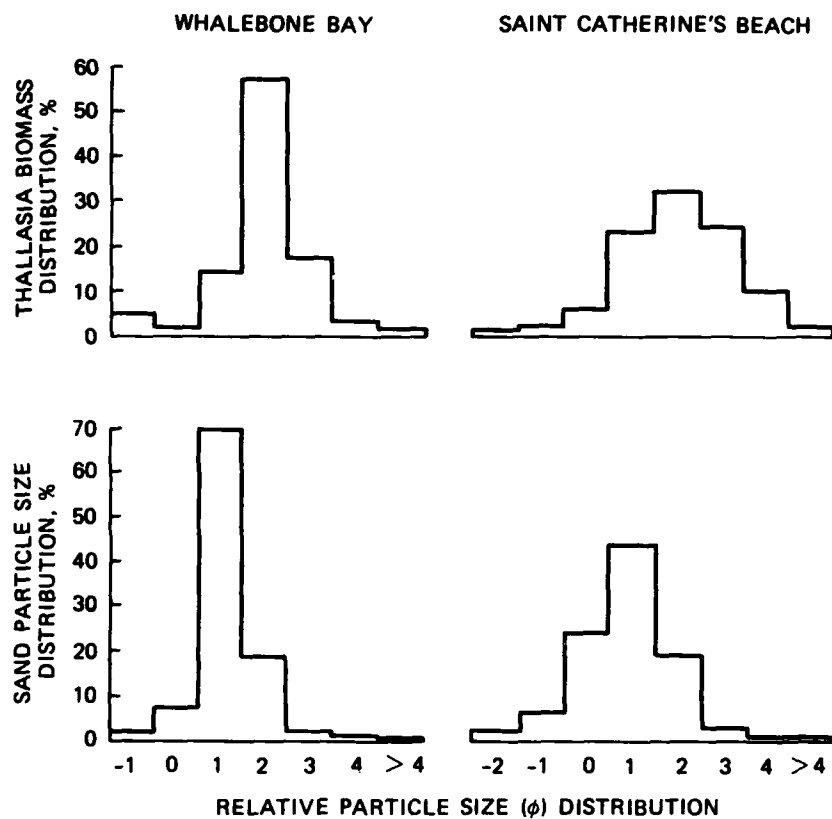variety of substrates from pure firm sand to pure

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Figure 3-15. Sediment particle size versus *Thalassia* biomass
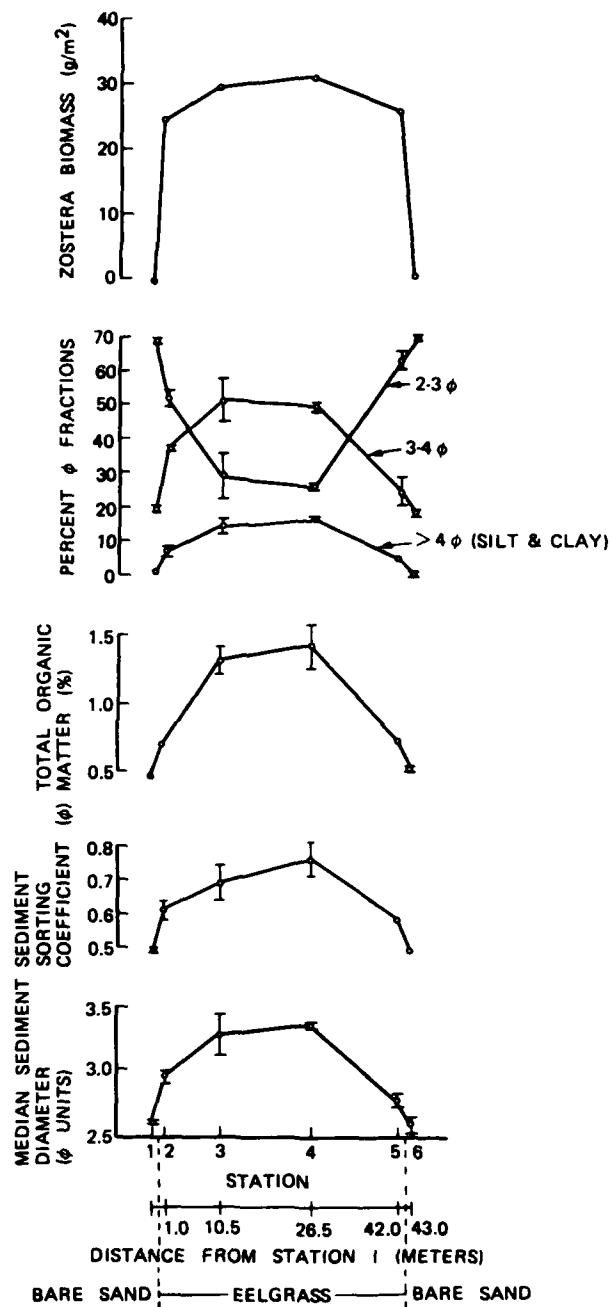distributions at two stations in Bermuda (after Orth 1977b)

Figure 3-16. Sediment particle size distribution and eelgrass biomass gradients from a transect study across a seagrass bed (after Orth 1977a)
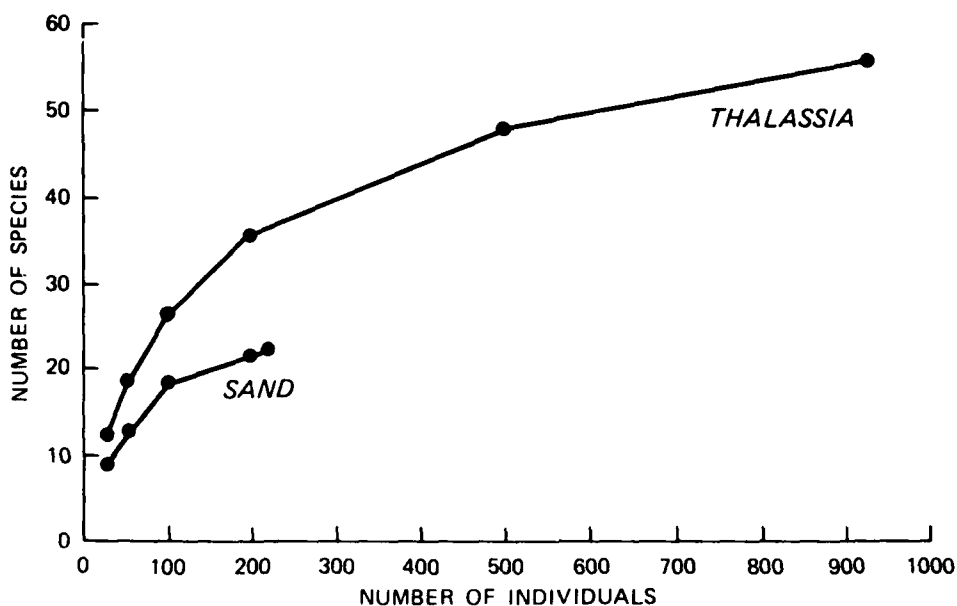
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Figure 3-17. Rarefaction curves (Sanders 1968) for *Thalassia* and
sand stations in Whalebone Bay (after Orth 1977a)

soft mud (Phillips 1974), although it appears to
favor sandy substrates (greater than 70 percent
sand) (Orth 1973, 1977a). Subtropical seagrasses
in Florida are reported from fine to coarse sand
(Stoner 1980, Santos and Simon 1974, Holm 1978,
Young and Young 1977).

(2)   Sediment depth is critical to the growth of turtle
grass which has a dense rhizomal and root system,
and may bind the sediment to a depth of 1.2 to
1.8 m below the surface (Thorhaug 1981). Zieman
(1972) has found turtle grass roots as deep as
4-5 m. This species does not grow well in shallow
sediments. Figure 3-18 shows the effect of sedi-
ment depth on turtle grass standing crop biomass
and associated macrobenthos. Figure 3-19 shows
the relationship of sediment depth to turtle grass
blade density and length (Zieman 1975). Other sub-
tropical seagrass species (e.g. *Halodule* and
Syringodium) have rhizome and root systems which
only penetrate a few centimetres below the surface
of the sediment (Thorhaug 1981). The lack of suf-
ficient substrate depth has been cited by Thorhaug
(1981) as a primary reason for the patchiness of
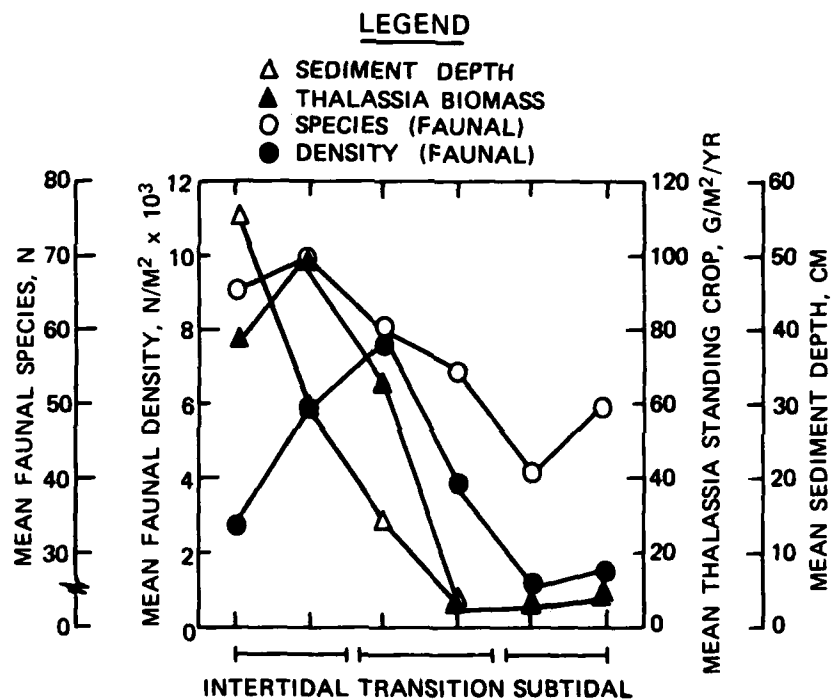turtle grass *Thalassia* in Florida waters.

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Figure 3-18. Mean macrobenthic faunal density and number
of species along an environmental gradient of varying
sediment depth and turtle grass (*Thalassia*) biomass
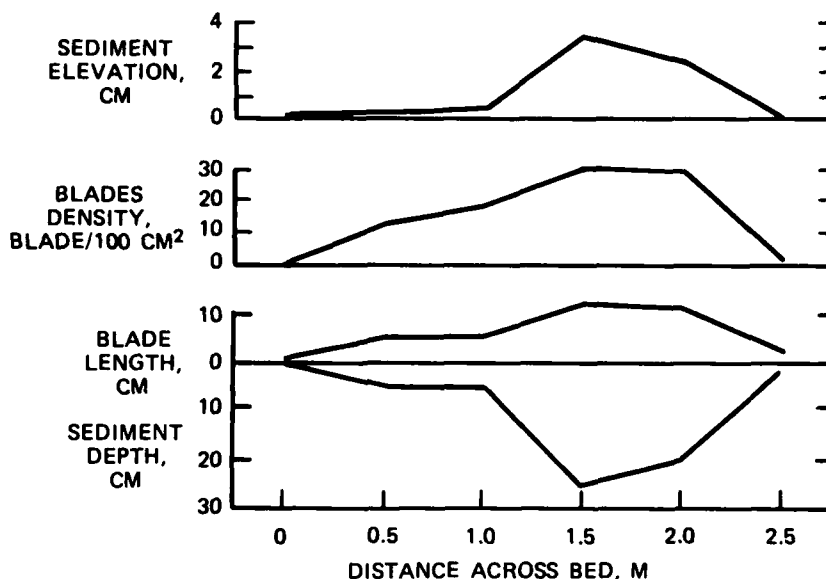(data from Holm 1978)

Figure 3-19. Relationships between depth of sediment, length and density of *Thalassia* blades, and sediment elevation caused by sediment stabilization in a bed off Key Largo, Florida (after Zieman 1975)

(3) In kelp habitats, kelp survival depends on the presence of a suitable hard rock or compacted solid substrate. Shifting sand bottoms (storm or tidally induced) will cause the disappearance of this habitat type (Phillips 1974) if exposed surfaces are covered with sediment.

c. Reef. Substrate quality is very important in determining the distribution of biological reefs. Oyster, coral, and worm (sabellariid) reefs are distributed in a wide variety of substrates from rock/hard bottoms to unconsolidated bottoms ranging from sand to mud. Oysters may grow equally well on a hard, rocky bottom or on semihard mud firm enough to support their weight. Shifting sand and soft mud are the only types of bottoms which are totally unsuitable for oyster communities (Galtsoff 1964). Planktonic larvae of oysters, coral, and sabellariids require the presence of a suitable hard substrate and usually settle on or near well-established populations of their own species. Larvae of these reef-building species do not successfully settle on unconsolidated sediments directly, as they would be smothered by fine, silt-size particles; these larvae generally settle on

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shells, rock surfaces, or other suitable debris serving
as "terra firma." The seaward extension or development
of a fringing coral reef is dependent on the buildup of
dead coral and algal sediments along its seaward edge.
This is depicted in Figure 3-20, which shows the exten-
sion of reef as a function of the buildup of dead coral/
algal rock and sediments on its seaward edge to depths
of 90 ft or less (Smith 1971; Goreau, Goreau, and Goreau
1979). Sabellariid worm reef habitats are markedly af-
fected by substrate quality in as far as the worms exert
a bias in their choice of tube-building materials and
their requirement for high energy environments (Scholl
1958, Kirtley and Tanner 1968, Rees 1976). The worms
seize and sort suspended sand-size particles from the
turbulent waters and fix appropriately shaped particles
to their cylindrical tubes (Figure 2-10) with a special
protein cement, which the animals secrete (Vovelle 1965).
The worm reefs consist of agglutinated quartz grains,
heavy mineral grains, small fragments of comminuted
mollusk shells (shell hash), and other detrital frag-
ments such as ostracods, foraminifera tests, fecal pel-
lets, and sponge spicules (Kirtley and Tanner 1968).
The availability of suitable substrates for the estab-
lishment of biological reefs is dependent on relatively
high wave or current energy environments, and they are
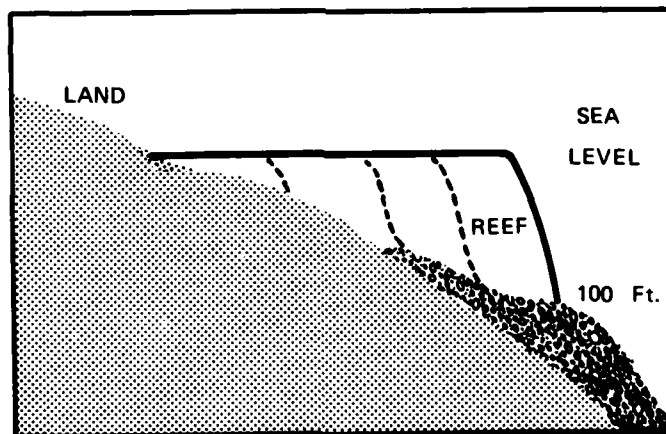distributed accordingly.

Figure 3-20. Schematic illustrating the growth and development of a
fringing reef. Broken lines indicate successive stages of growth
from left to right as coral broken by wave action builds up a base
of dead coral substrate sufficiently shallow (less than 100 feet) to
enable vigorous coral growth (after Smith 1971)

d. Rock/hard bottom habitat. The availability of suitable hard substrates for the establishment of fouling or sessile benthic communities is largely regulated by current and wave energies necessary to maintain a relatively clean hard substrate. The distribution of rock/hard substrates in estuarine and coastal marine environments is generally limited to moderate to high current/wave energy areas with relatively low light intensities and/or high turbidity levels. Substrate factors such as texture, chemistry, orientation (vertical, horizontal, etc.), color, and cleanliness will affect settling of larvae onto hard substrates and thereby influence the community structure and composition.

Vegetation Quality

56. Qualitative vegetation factors such as blade density; blade size, length, and width; and root depth influence the distribution composition and structure of benthic communities associated with submerged vegetated habitats (i.e. seagrasses and kelp). Standing vegetation serves as both a substrate for attached sedentary and motile epifaunas and epiphytes and as a food source (directly grazed or indirectly consumed as detritus). Seagrasses are very important in stabilizing unconsolidated bottoms by binding the sediments with their roots and rhizomes. Seagrass blades serve as baffles to deflect currents and trap sediments, thereby reducing turbidity levels in water passing through a seagrass bed (Zieman 1975; Phillips 1974, 1978, 1980). Qualitative differences in seagrass species (i.e. blade size, length, and width) and vegetation densities in turn affect the qualitative and quantitative nature of associated macroinvertebrate communities by increasing the habitat structural diversity and complexity compared with unvegetated habitats (see Figure 3-17). Qualitative and quantitative differences in seagrass animal communities have been observed for tropical, subtropical, and temperate seagrass systems. For example, in subtropical seagrass habitats, Thorhaugh (1981) found the most abundant and diverse animal communities associated with turtle grass (*Thalassia*), followed by manateegrass (*Syringodium*), while shoalgrass (*Halodule-Diplanthera*) contained substantially lower animal biomass

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and numbers of macroinvertebrate species. A comparative study of
Florida turtlegrass, shoalgrass, and sand habitats by O'Gower and
Wacasey (1967) found greater numbers of macroinvertebrate species in
turtlegrass habitats, with decreasing species richness in shoalgrass
and sand habitats. Densities of faunas were generally higher in shoal-
grass habitats in this study than in turtle grass, while sand habitat
densities varied appreciably between high and low current stress areas
(Figure 3-21). Sharp qualitative differences in major taxa were ap-
parent between vegetated and unvegetated-sand bottoms at both locations.
Stoner (1980) studied the structure of seagrass benthic communities as
a function of seagrass biomass and found significant faunal differences
between heavily vegetated bottoms and a relatively bare sand bottom,
although no significant differences were found between number of spe-
cies, faunal densities, and faunal biomass with increasing vegetation
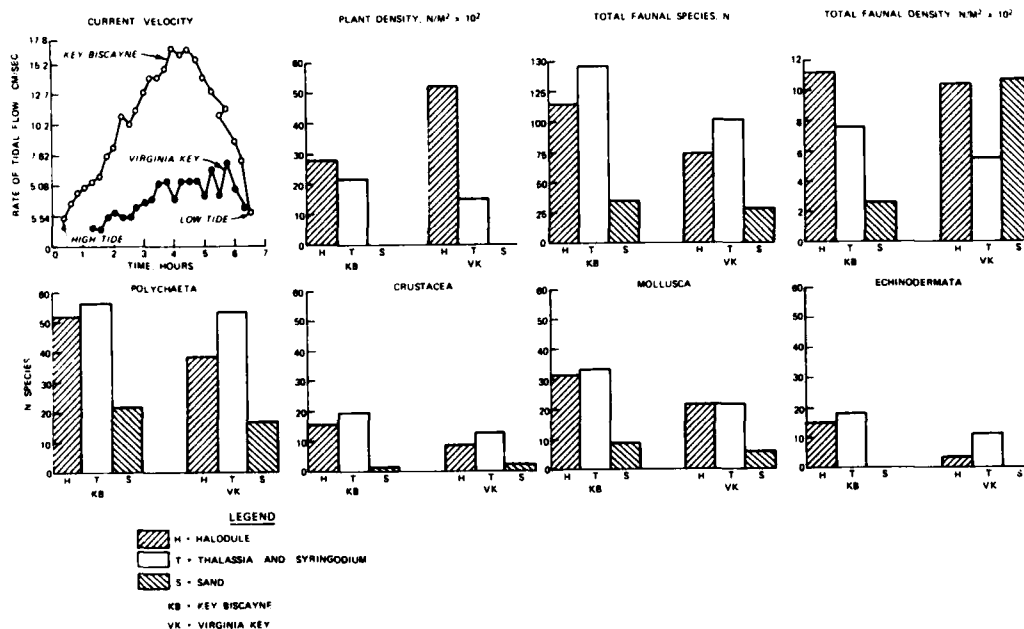cover (*Thalassia* density). Slight reductions in faunal biomass were

Figure 3-21. Comparative effects of current stress on macrobenthos
from three habitat types in a subtropical marine coastal environment
(data from O'Gower and Wacasey 1967)

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observed as turtle grass biomass increased (Figure 3-14). In turtle grass beds, leaf density largely determines the ability of the community to reduce water flow, promote sedimentation, and stabilize the sediment surface (Zieman 1975). Stoner (1980) found faunal similarities within turtle grass habitats of different plant densities, which were distinct from the largely unvegetated site. Polychaetes and amphipods made up the bulk of the macrobenthic community in numbers of species, density, and biomass (Figure 3-14). This contrasts with Brook's (1978) study of turtle grass communities in Biscayne Bay, where he found low faunal similarity within five turtle grass habitats of similar plant densities (>3000 blades/m^2) and large differences in faunal composition and abundance among sites (Table 3-6). Macroinvertebrate densities ranged from 292-10,644/m^2, while taxa compositions were highly variable among sites. Site descriptions for this study indicate varying sediment depths, sediment composition, and blade lengths of turtle grass, suggesting substrate quality may be more important than plant densities in structuring the turtle grass benthic communities at each site. Sediment depth has already been mentioned (see substrate quality, paragraph 55b(2)) as a limiting factor for turtle grass distribution and cover and may have a significant effect on the distribution and abundance of macrobenthic invertebrates, as was found by Holm (1978) in Biscayne Bay, Florida (Figure 3-18). Brook's study was conducted in the same bay, where differences in sediment depth and quality were not apparently related to turtle grass blade densities but may have been partially responsible for the observed faunal variability. In subtropical seagrass systems, blade density and length appear to be related to sediment depth, as shown in Figure 3-19. Increasing densities of seagrass leaves increase the surface area of the community and in turn offer greater substrate for epiphytes and epifaunas, as well as providing denser habitat for the organisms that use the grass beds as a nursery and for shelter (Zieman 1975).

57. Temperate seagrass beds dominated by eelgrass (*Zostera*) show marked seasonal changes in standing crop biomass and corresponding fluctuations in associated invertebrate and fish communities. Thayer,

Table 3-6

Comparative Macrofaunal Abundances in Turtle Grass Communities with High Blade Densities (>3000 m^2), Biscayne Bay, Florida (after Brook 1978)

Parameter	Stations				
	Beak Cut	West Point	Featherbed Bank	Long Arsenicker	Murray Key
Blade length, cm	30	40	30-50	25-40	>60
Sediment depth, cm	5	--	25	10	15
Sediment classification	Sand, coarse rubble	Floc. and rubble	Soft carbonate, flocculant material	Fine floc. and rubble	Fine floc. material
Total fauna: no. of species (N)*	80	61	38	72	52
Total faunal density, N/m^2	10,644	4286	292	1010	4508
Mollusks, %	7	25.5	52	32.5	71.5
Polychaetes, %	31.3	10.5	20.5	33.7	14.5
Crustaceans, %	57.5	57.1	15.7	24.4	11.4

* 161 macroinvertebrate species collected at all stations.

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Adams, and LaCroix (1975) found a close relationship between eelgrass
biomass and epifaunal invertebrate densities and fish biomass within a
Zostera bed (Figure 3-22). Their study indicated that declines in in-
vertebrate abundances were coincident with increases in fish biomass,
particularly the pinfish, *Lagodon rhomboides*, within the eelgrass beds,
suggesting heavy predator pressure on epifaunas during periods of
highest eelgrass biomass. A trawling study by Orth and Heck (1980) and
Heck and Orth (1980) in eelgrass beds from the Chesapeake Bay also
found concomitant increases and decreases in numbers of fish and decapod
crustacean species and their abundances which were directly correlated
with temperature and eelgrass biomass changes throughout the year. Peak
changes occurred during spring and summer, and lows during fall and
winter. Marked differences were noted in eelgrass fish community struc-
ture between North Carolina and Chesapeake Bay, most notably in the
scarcity of the pinfish (*L. rhomboides*) in Chesapeake Bay. This
species is considered to be a major predator and determinant of epifau-
nal community structure in seagrass beds where it is abundant (Darnell
and Wissing 1974, Orth and Heck 1980). Nocturnal abundances of fish
and decapod crustacea were much greater than diurnal abundances, high-
lighting the significance of seagrass beds in providing refuges for
relatively mobile species, such as shrimp, crabs, and fish. Relatively
large variations in macroinvertebrate abundance have been observed be-
tween different eelgrass habitats, not unlike those found in tropical
and subtropical seagrass habitats (Heck 1977, Young and Young 1977,
Stoner 1980, Santos and Simon 1974, Brook 1978). Thayer, Adams, and
LaCroix (1975) reported relatively low faunal densities and biomass from
the Newport River estuary in North Carolina, averaging 923 individuals/
m^2 and 7.5 g/m^2 (AFDW), respectively. However, Marsh (1973) observed
mean epifaunal densities of 9600 m^2 in eelgrass beds from the York
River in Virginia, while Orth (1973) reported a mean infaunal density
of 15,000/m^2 in Chesapeake Bay. In every case, interhabitat compari-
sons between vegetated and unvegetated bottoms have shown markedly
larger numbers of species, faunal abundances, and biomass within vege-
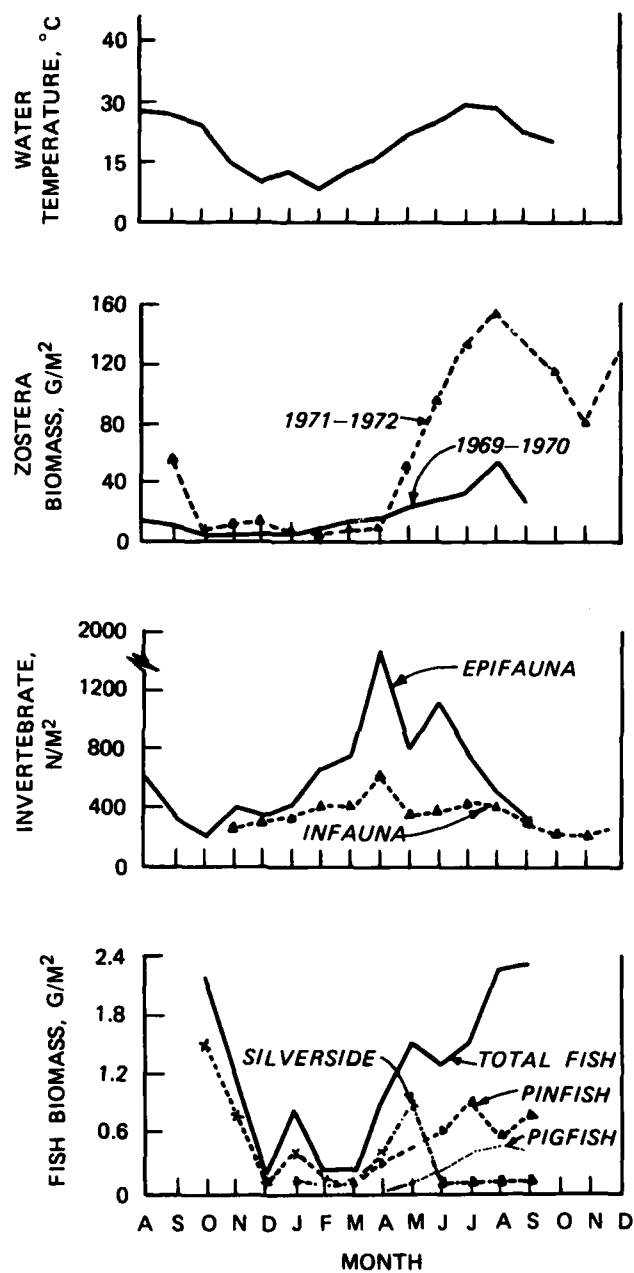tated habitats. This was graphically illustrated in a study by Orth

Figure 3-22. Seasonal distribution of water
temperature, *Zostera* dry-weight biomass, mean
empfaunal and infaunal densitites, and major
fish species biomass (after Thayer, Adams,
and LaCroix 1975)

(1977a) of an eelgrass bed (Figure 3-23; Figure 3-16) and a turtlegrass bed (Figure 3-17). His study showed that numbers of faunal species and abundance increased as plant densities increased. Figure 3-24 shows the seasonal abundance and numbers of organisms per gram of *Zostera* at three different depth locations (Marsh 1973). This study indicates faunal densities increase on each *Zostera* blade as plant densities decline on a seasonal basis. Recent studies in transplanted eelgrass meadows from North Carolina (Fonseca et. al 1979; Kenworthy et al. 1980; Homziak, Fonesca, and Kenworthy 1982; Homziak, Fonseca, and Kenworthy
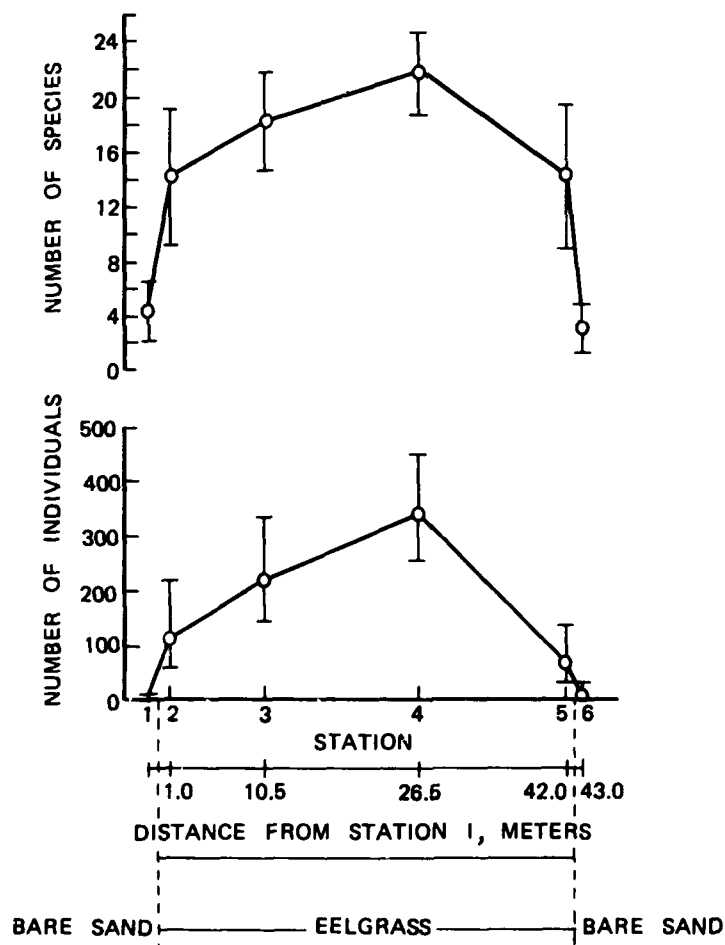
Figure 3-23. Mean and range of macrobenthic species and number of individuals collected at transect stations across an eelgrass bed (after Orth 1977a). Compare with Figure 3-16

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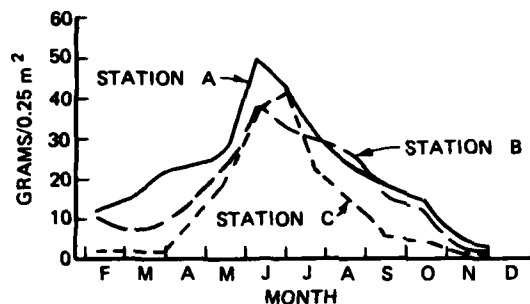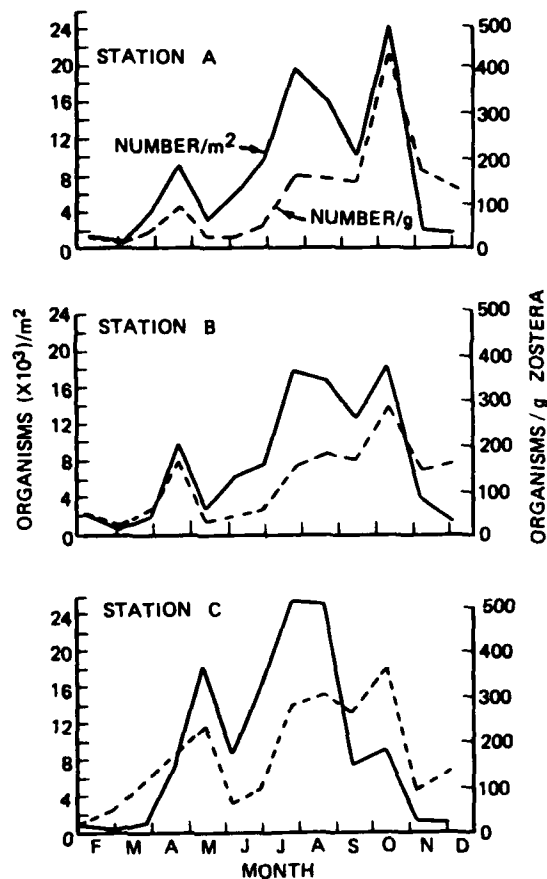
Figure 3-24. *Zostera* density-dependent faunal benthos chang:s:
(a) seasonal *Zostera* biomass; (b) comparative seasonal chang¢s
in numbers of macrobenthos per gram of *Zostera* and macrobenthos
density (number/m^2) from three stations (A = 0.7 m; B = 1.2 m;
C = 1.6 m) at three water depths (after Marsh 1973)

in review) have shed light on macrobenthic community structure and its development as a function of eelgrass shoot density. Homziak, Fonseca, and Kenworthy (1982) found macrofaunal density, number of species, and diversity positively but nonlinearly correlated with increasing eelgrass shoot density in a developing meadow. They also found a nonlinear decrease in dominance with increased shoot density. Another aspect of the same study (Homziak, Fonseca, and Kenworthy in review) demonstrated recruitment into and increased survival of juvenile hard clams (*Mercenaria mercenaria*) within transplanted eelgrass plots compared with unvegetated areas. Peterson (1982) found the clams *M. mercenaria* and *Chione cancellata* positively associated with *Halodule wrightii* cover in North Carolina, and high rates of mortality when vegetation was experimentally removed. High mortality rates were primarily attributed to predation.

58. The significance of seagrass in consolidating and stabilizing sediments is well established, and the loss or destruction of seagrass habitats may result in substantial substrate erosion (Phillips 1974, Zieman 1975, Christiansen et al. 1981). Physical destruction of stable eelgrass beds in the York River, Virginia, by the cownosed ray (*Rhinoptera bonasus*) caused marked decreases in faunal diversity and densities and the vegetation beds were replaced by unstable sand habitat (Orth 1975). Wilson (1949) noted that sand banks were lowered by 2 ft or more following the disappearance of eelgrass in England. The ability of seagrasses to stabilize and consolidate sediments is a function of their root and rhizome density and depth of penetration into the substrate. Species such as *Thalassia* and *Zostera* are important sediment stabilizers because of their wide distribution in tropical, subtropical, and temperate environments. Faunal changes following the disappearance of seagrass habitats have been much studied in the case of the rapid decline of eelgrass beds during 1931 along the Atlantic coasts of North America and Europe. In one year almost 99 percent of the standing stock of eelgrass was destroyed by a disease called "wasting disease." Epifaunas associated with eelgrass rapidly disappeared, while commercial fish and shellfish suffered large population

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declines. Waterfowl dependent on this plant for food also suffered tremendous population declines (Phillips 1974, 1978).

Temperature

59. Temperature is a major water quality factor structuring benthic communities in estuarine and marine systems (Gunter 1957, Hedgpeth 1957). The magnitude of diurnal and seasonal temperature changes generally increases from the tropics toward the arctic and from deepwater to shallow-water environments, while temperature fluctuations are generally more stable at the mouths of estuaries than at the upper reaches (Day 1951). Temporal shifts in temperature on the east coast are primarily caused by seasonal fluctuations in strongly flowing air masses, whereas west coast, temperature changes are primarily brought about by upwelling and injections of cold water from the sea (Odum and Copeland 1974). Seasonal temperature changes are generally greater on the east coast than on the west coast at similar latitudes. In marine coastal environments, away from high-energy beaches and salinity-shocked river mouths, salinity and high-energy wave stress diminish and latitudinal temperature and light programming become more important in the distribution and zonation of benthic communities (Odum and Copeland 1974).

60. Between the latitude of Alaska, where winter ice is prevalent, and the latitude of southernmost Florida are the temperate marine coastal ecological systems, characterized by sharp seasonal pulses in light energy and temperature. The magnitude of the seasonal pulse generally increases northward to Maine and southern Alaska. At tropical latitudes south of Florida, seasonal pulses in light energy and temperature diminish markedly and temperatures are relatively uniform. Figure 3-25 depicts average latitudinal temperature ranges for the Pacific and Atlantic Oceans and corresponding light intensity shifts. This demonstrates the close relationship between radiation income fluctuations in the oceans and corresponding temperature changes. Oceans in the northern hemisphere exhibit larger temperature fluctuations, particularly at higher latitudes, because seasonal shifts in prevailing wind
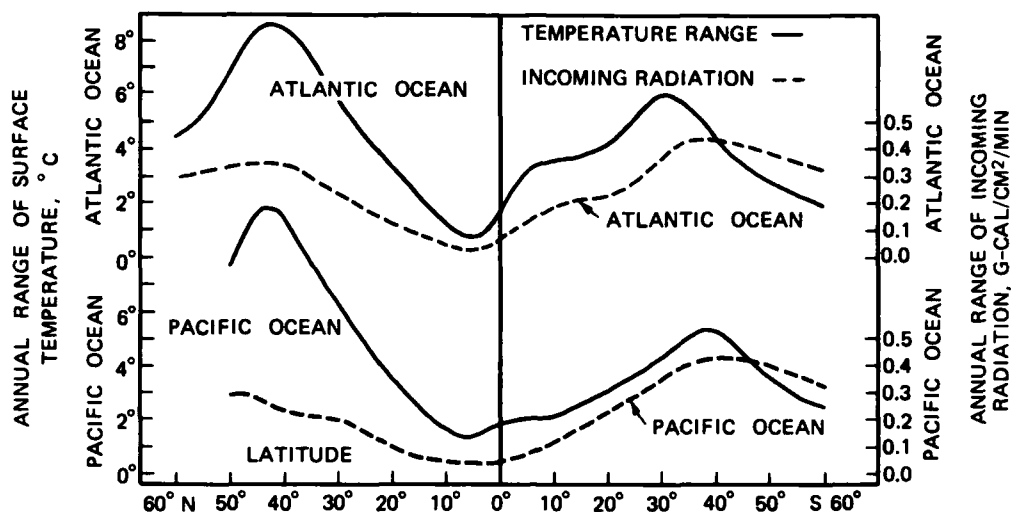
Figure 3-25. Average annual ranges of surface temperature in the Atlantic and Pacific Oceans plotted against latitude and corresponding ranges in the radiation income (after Sverdrup, Johnson, and Fleming 1942)

patterns blow cold winds from the continents toward the oceans and thereby greatly reduce winter temperatures (Sverdrup, Johnson, and Fleming 1942). Comparative annual variations in temperature at depth from different latitudes show generally increasing seasonal variations with increasing latitude (Figure 3-4). Bottom temperatures at depths of 15 to 44 m north of Cape Hatteras are generally more than 4° C cooler than surface waters between May and September (seasonal thermocline) (Emery and Uchupi 1972). Temperatures for coastal waters near Portland, Maine, range annually from 2.8° to 15.5° C (Δ temperature = 12.8° C), while they range only from 24.4° to 29.6° C (Δ temperature = 5.2° C) near Miami, Florida. For most of the northeast Pacific coast, mean high and low temperatures range from 9° to 14° C, with a mean annual range of only 5° C (Bourke, Glenne, and Adams 1971). Due to summer upwelling along the Pacific coast, lowest temperatures generally occur during summer (Bourke, Glenne, and Adams 1971).

61. The broad latitudinal distribution or range of benthic species is largely controlled by temperature, whereas salinity and

substrate quality largely determine their microdistributional patterns at a given latitude within an estuarine or marine system (Jones 1950, Thorson 1955, Hedgepeth 1957, Wells 1961). Biogeographical provinces or zones of faunal/floral similarity are based on faunal/floral distribution patterns in relation to temperature regimes to which many species are correlated due to physiological adaptations for maintenance, enzyme operation, seasonal programming of reproduction, and common access to genetic pools (Odum and Copeland 1974) (Figure 3-26). Broad regions of faunal overlap generally exist between contiguous biogeographical provinces. On the western Atlantic continental shelf, for example, south of Cape Hatteras, Gulf Stream eddies moderate temperature fluctuations near the seaward edge of the continental shelf such that many Caribbean (tropical) species range into what is generally characterized as the Carolinian Province (Pearse and Williams 1951). Tropical and polar organisms live in a relatively constant thermal range and have a limited ability to alter their metabolic responses to different temperatures outside their accustomed range in an adaptive or compensatory manner. In contrast, most temperate zone organisms are able to acclimate and have evolved homeostatic mechanisms enabling them to be partially insensitive to temperature fluctuations (Vernberg 1981). Figure 3-27 graphically depicts this metabolic temperature response pattern in tropical, polar, and temperate zone organisms. Seasonally programmed spawning and reproductive cycles become increasingly more common in faunas with increasing latitudes toward the arctic. Therefore, seasonally programmed faunal pulses (recruitment) are common at temperate and arctic latitudes. At temperate and boreal (northern) latitudes, seasonal spawning pulses of benthos occur in late spring and early summer. Sometimes a smaller peak may also occur in late summer to early fall. Migrations of animals coinciding with seasonal temperature changes often include many predators of estuarine and marine benthos (Day 1951). Migrations of invertebrates and fishes into deeper and warmer offshore waters in winter have also been reported (Kinne 1963). This contrasts sharply with tropical marine and estuarine ecosystems, where most species do not exhibit sharp seasonal reproduction and
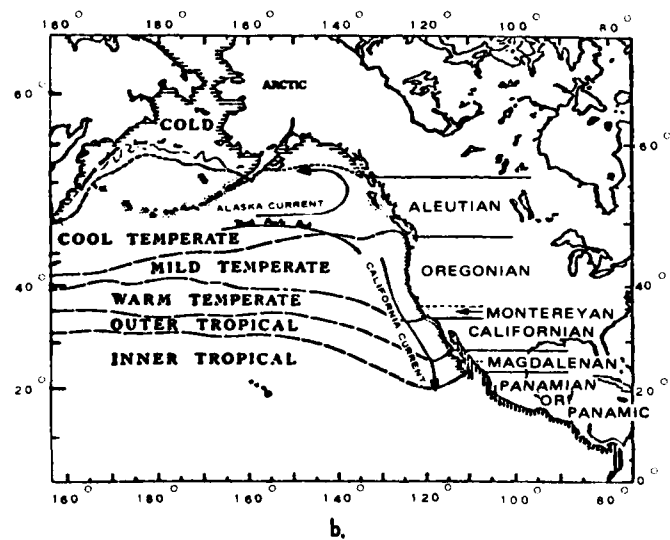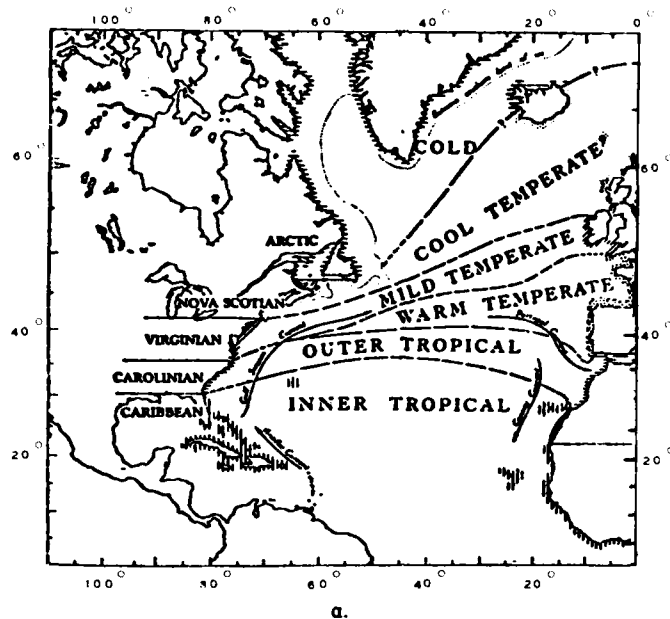
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Figure 3-26. Biogeographical provinces related to temperature
regimes and faunal/floral similarities: (a) western north At-
lantic; (b) eastern north Pacific (after Hall 1964)

HIGH ↑

METABOLIC RESPONSE

a = POLAR REGIONS
b = TEMPERATE ZONE
c = TROPICS

b

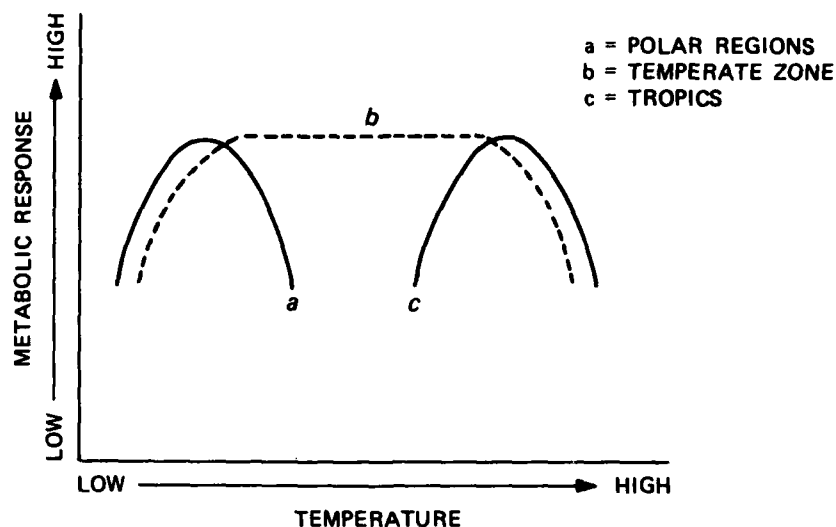a   c

LOW

LOW ————————————→ HIGH

TEMPERATURE

Figure 3-27. The generalized metabolic response to temperature
of animals from different climatic regions

spawning cycles because of relatively stable temperature and light con-
ditions. Recruitment of larvae at tropical latitudes is generally
continuous throughout the year. There is also a generally recognized
pattern of decreasing numbers of invertebrate species, especially epi-
faunal species, with increasing latitudes (i.e., from the tropics to
the arctic) in marine coastal environments (Carriker 1967). It is
likely that this same trend exists in estuaries as well, especially in
shallow areas subject to temperature extremes and ice stress. Benthic
species with pelagic larvae decrease in abundance generally from tropi-
cal latitudes to the polar regions. Thorson (1957, 1958, 1961) reports
that 90 percent of tropical species exhibit pelagic (planktonic) larval
stages, compared with approximately 67 percent in temperate marine
coastal areas, dropping off to only a few species in polar waters. It
is also likely that a similar latitudinal gradient in larval type
(planktonic versus nonplanktonic) may be present in estuarine environ-
ments due to general increases in salinity and temperature stresses
with increasing latitude. Species that brood their young (nonplank-
tonic, K-strategists) would be favored at lower temperatures character-
istic of polar environments over those that release large numbers of

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planktonic larvae (r-strategist)(Southwood 1977, Clarke 1979).

62. It is also generally recognized that organisms living in tropical marine and estuarine environments live much closer to their upper thermal limits than those living at temperate latitudes (Zieman 1970, Thorhaug 1981); at high arctic latitudes, however, ice stress may severely limit the distribution of epifaunas in shallow littoral areas less than 10 m deep (McRoy and Allen 1974). Thermal stress may be potentially more damaging to benthic organisms living at tropical latitudes compared with temperate latitudes, and the siting of power plants near tropical estuaries with resulting thermal releases may act as a severe stress (Odum 1971, Zieman 1970). Mortalities associated with cold temperatures have been reported for invertebrates and fish along the Georgia coast and estuaries (Dahlberg and Smith 1970), western Florida coast (Storey 1937, Springer and Woodburn 1960), Florida bay (Tabb, Daubrow, and Manning 1962) and the Texas coast (Gunter and Hildebrand 1951).

    a. Unconsolidated soft bottoms. Temperature ranges found in a given area will affect the distribution of benthos in soft bottom habitats. The temperature tolerances of individual species will determine the distributions observed. The number of infaunal species observed along the latitudinal gradient increases gradually toward the equator, although not nearly to the degree that epifaunal species increase (Thorson 1961,*). In shallow estuarine and marine soft bottom habitats, temperature stresses may affect infaunal and epifaunal invertebrates differently. At arctic latitudes burrowing infauna may survive temperature extremes and ice stress, whereas epifauna may not. At lower latitudes, infauna may escape high temperatures by burrowing deeper within the sediments, whereas epifaunal invertebrates are subject to the full temperature regime. Estuaries and marine areas characterized by relatively poor water circulation during summer months may become thermally stratified, resulting in oxygen-poor reducing conditions in benthic environments. Biggs (1967) reported sediments in Chesapeake Bay below the 50-ft contour were generally oxygen deficient and reducing during the summer months, while those observed in depths less than 40 ft were oxygenated

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continuously. Oxygen depletion has also been observed
in the New York Bight (Boesch in press, Malone 1978).
Thermal stratification with low oxygen levels will have
a marked effect on the distribution of benthos in those
areas, generally resulting in an impoverished benthic
fauna or its complete elimination during the summer
months (Holland, Mountford, and Mihursky 1977). Standing
crops for benthos in unconsolidated sediment(s) in shal-
low marine coastal environments (10 m) average 450 g/m^2
between Nova Scotia and New York, dropping to 250 g/m^2
between New York and Cape Romain, and average 100 g/m^2
between Cape Romain and Key West, Florida (Emery and
Uchupi 1972). Thus, sharp contrasts in observed benthos
standing crop exist along latitudinal gradients on the
western north Atlantic shelf; similar, but less pro-
nounced, biomass gradients probably occur along the
West Coast as well.

b. <u>Submerged aquatic vegetation habitats</u>. Temperature
broadly delimits the geographical distribution of sea-
grass and macroalgae species (see paragraphs 30-32 and
36). Temperature, light intensity, salinity, and
substrate quality are the factors principally responsible
for the distribution of all the species making up vege-
tated bottoms. In subtropical and tropical estuaries,
seasonal pulses of vegetation are less apparent than at
temperate latitudes, where large temporal variations in
submerged vegetation biomass occur. (See Figures 3-22
and 3-23 for an illustration of eelgrass temporal varia-
tions and corresponding variations in macroinvertebrate
biomass.) Corresponding temporal variations in macro-
invertebrate community structure are generally much
greater in temperate eelgrass beds than in tropical sea-
grass beds. A recent study by Heck and Orth (1980) doc-
umented a temporal and latitudinal gradient in decapod
crustacean abundances between Chesapeake eelgrass beds
and tropical seagrass beds. They found that decapod
crustacean abundances were positively correlated with
plant biomass throughout the year and that total abun-
dances of decapods were much greater in Chesapeake Bay
eelgrass beds than those reported from North Carolina
eelgrass habitats or Gulf of Mexico turtle grass habi-
tats. Corresponding temporal variations in turtle grass
biomass and associated epiphytes occur in subtropical
estuarine and marine coastal environments, although
vegetation is present throughout the year (Figure 3-28).
Lethal temperature limits for subtropical-tropical
seagrasses are only a few degrees above their ambient
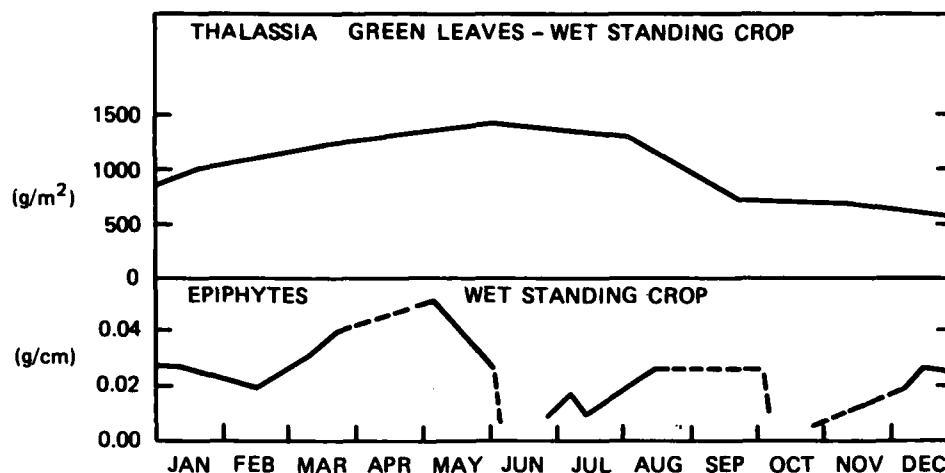temperature, which is between 32° and 34° C (depending

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Figure 3-28. Seasonal biomass distribution of *Thalassia testudinum* and associated epiphytes from a south Florida estuary (after Jones 1968)

on geographical location) (Thorhaug 1981). Wigeon grass (*Halodule*) has an upper temperature limit of perhaps 1° C greater than turtle grass (*Thalassia*), while manateegrass (*Syringodium*) appears to be more sensitive than turtle grass, with an upper limit of between 30° and 33° C. The latitudinal distribution of marine kelp beds is limited by individual species tolerances to temperature (also by ice stress in Alaska (McRoy and Allen 1974)), while the seaward distribution is generally limited by available substrate, turbidity, and depth (Phillips 1974). Light intensity rather than temperatures per se regulate many aspects of kelp growth and development (North 1964, 1966).

c. Reef habitat. The distribution of biological reefs (oyster and sabellariid) in estuaries is not generally limited by temperature, although temperature and light intensity may regulate spawning cycles. Oyster reefs exhibit wide distributions in Atlantic, Gulf, and Pacific estuarine environments. They generally exhibit wide temperature tolerances and are considered eurytopic species. Stenzel (1971) attributes the wide geographical range (8050 km, Figure 2-6) of the American oyster primarily to its tolerance to low temperature. Oysters are known to live in temperatures varying from 1° to 36° C throughout their geographical range (Galtsoff 1964). The northern limit of commercially harvested

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oyster grounds is Long Island Sound (lat. 41° N) and the
southern limit is close to Apalachicola Bay, Florida
(lat. 30° N), although productive reefs also occur in
Texas bays and in the Mississippi River Delta region
(lat 29° N) (Galtsoff 1964). Oysters cease feeding at
temperatures of 6° to 7° C. Maximum rates of feeding
occur at about 25° to 26° C and decline rapidly above
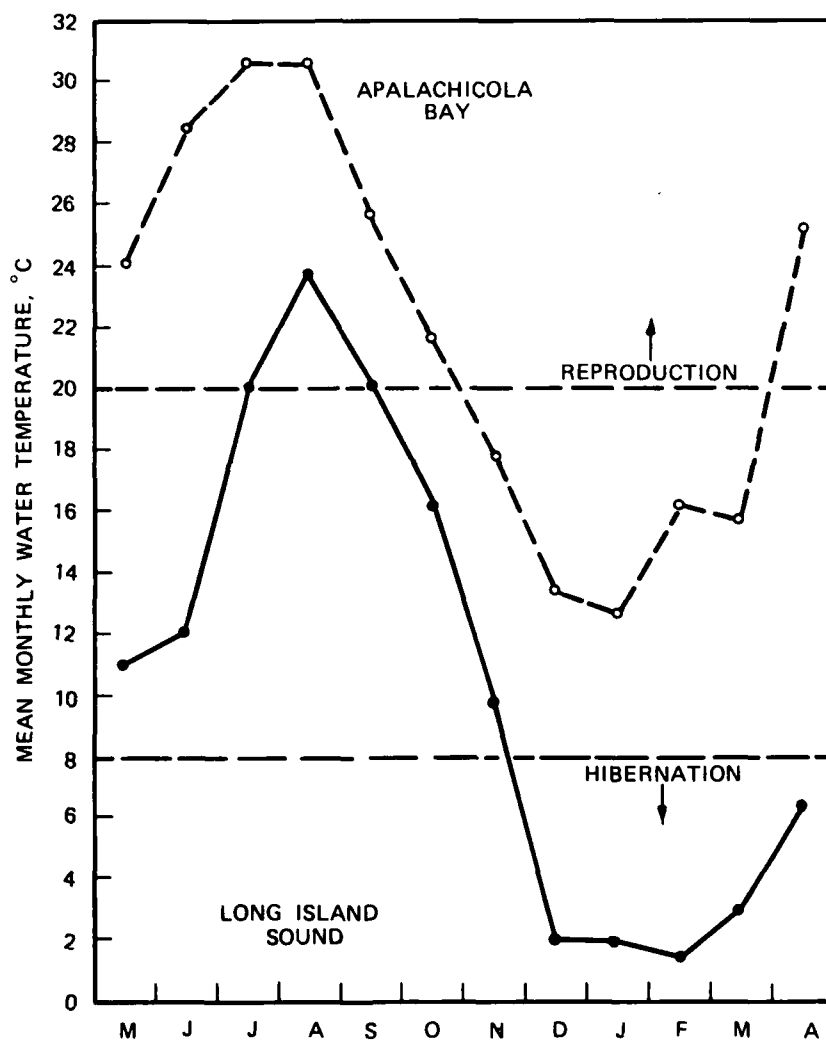32° C (Galtsoff 1964). Figure 3-29 shows the annual

Figure 3-29. Mean monthly temperature cycles in Apalachicola
Bay, Florida, and Long Island Sound, New York, illustrating
seasonal oyster activity and reproductive cycles (after
Galtsoff 1964)

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temperature cycles for both Long Island Sound and
Apalachicola Bay and illustrate the influences of
temperature on oyster populations living at each loca-
tion. Oysters in Apalachicola Bay continue to feed
year round and may reproduce 7 months out of the year,
spawning at temperatures of 20° C and above. At north-
ern latitudes such as Long Island Sound, the period of
feeding and growth is limited to about 6-1/2 months and
the oyster reproduction season is limited to only
around 2 months. An examination of thermal loading
effects of power plant discharge waters on oyster reef
communities from Crystal River, Florida, by Lehman
(1974), concluded that an average annual water tempera-
ture increase of 4° C increased oyster biomass, meta-
bolic rate, and turnover rate, but decreased the divers-
ity of the oyster reef community. High temperatures
during freshets may contribute to high oyster mortal-
ities, whereas oysters may withstand long periods of
low salinity at low temperatures (Galtsoff 1964).

(1) Oyster distributions may be limited in estuaries by
     diseases and predator pressure. Most oyster pred-
     ators and diseases are limited to salinities
     greater than 15 ^{o}/oo. Oysters weakened by the
     sporozoan parasite *Perkinsus marinum* exhibit mor-
     talities as high   60 percent during periods of
     high salinity and temperature (Mackin 1951).
     Another disease called MSX *(Minchinia nelsoni)* has
     caused significant mortalities in oyster reefs in
     the lower reaches of Chesapeake Bay and Delaware
     Bay. High temperatures during summer months are
     responsible for significant mortalities in diseased
     oysters in these areas. Studies of oyster reef
     macroinvertebrate communities by Wells (1961)
     showed sharp temporal shifts in invertebrate spe-
     cies as a response to seasonally programmed life
     cycles. Figure 3-8 depicts the mean number of
     species collected at each station per sampling date
     compared with the cumulative total number of species
     observed throughout the year, illustrating the
     dynamic seasonal changes occurring within the
     structure of an oyster community as a consequence
     of temperature and salinity fluctuations. Fig-
     ure 3-30 depicts the seasonal larvae set abundances
     of serpulids, oysters, and barnacles in a Texas
     estuary and illustrates the asynchrony in spawning
     cycles for some species (see also Figure 3-31).
     The distribution of biological reefs in marine
     environments are generally delimited by temperature,
     salinity, current and wave action, and turbidity.
     True coral reefs in particular are sharply limited

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Figure 3-31. Seasonal abundance patterns of fouling community larvae set near Beaufort Inlet, North Carolina (data from Woods Hole Oceanographic Institute 1952)
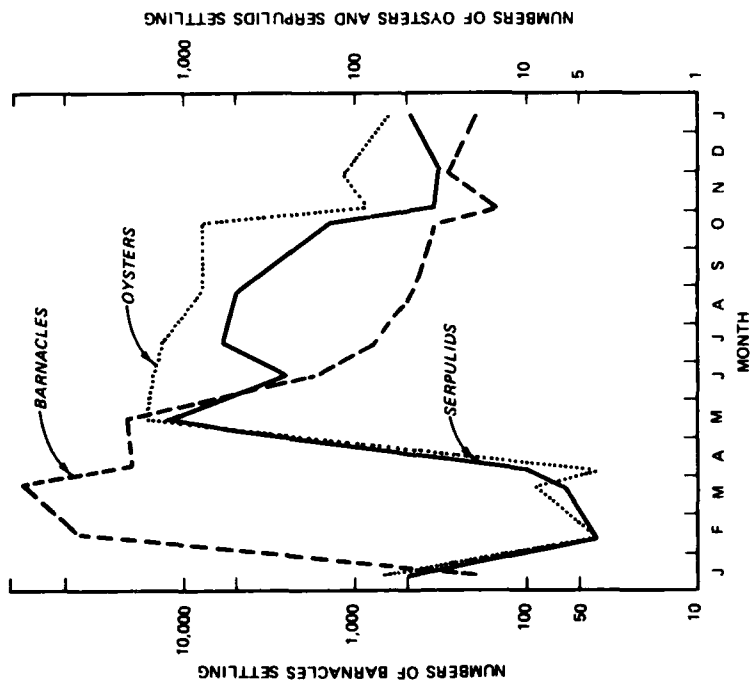

Figure 3-30. Seasonal spawning cycles (larvae set) for two reef-building species (oysters and serpulids) and one fouling species (barnacles) in Aransas Pass Inlet, Texas (after Behrens 1968)
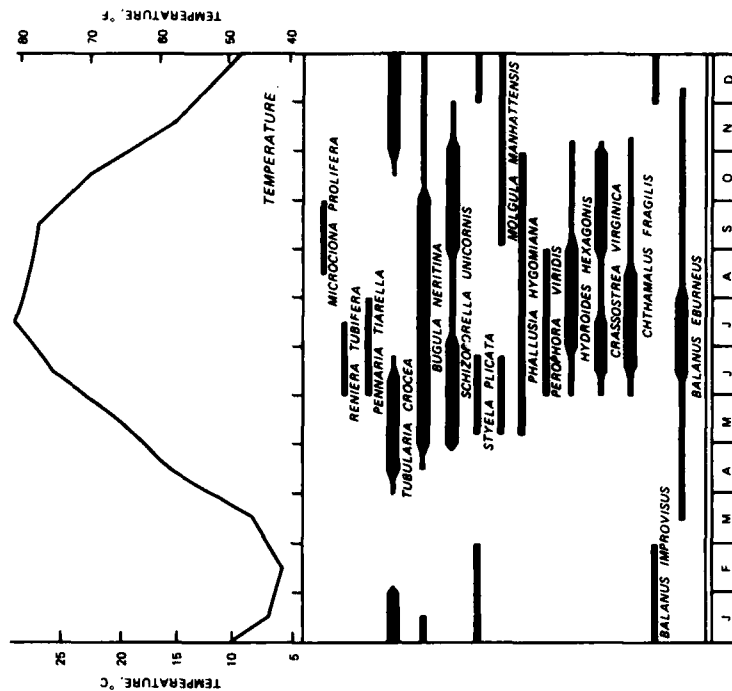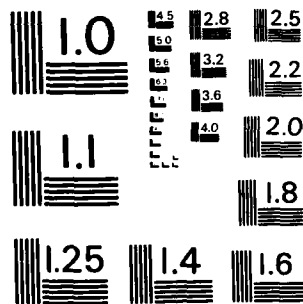
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cont,

MICROCOPY RESOLUTION TEST CHART

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by temperature and are only found existing within a temperature range from 16° to 36° C, optimum growth occurring between 23° and 25° C (Smith 1971). Sabellariid worm reefs are distributed between latitudes 72° N and 53° S and generally exhibit wide tolerances to temperature within their individual species geographical ranges.

d.   Rock/hard bottom habitats. Temperature fluctuations are important in regulating the structure of rock/hard bottom communities by seasonally programming the life cycles of many of the dominant species associated with this habitat type (Figure 3-31). However, species dominance hierarchies associated with fouling/hard bottom communities have been found to shift in an unpredictable manner, responding to the availability of hard substrates, interspecific competition, and predation (Sutherland and Karlsen 1977, Sutherland 1981, Menge and Lubchenco 1981), more so than to temperature per se. Temperature extremes in arctic and tropical latitudes may in turn severely stress epifaunal hard bottom communities in shallow littoral environments by mechanical removal (ice) or by exceeding lower or upper thermal tolerances; as a consequence epifaunal communities are much more diverse and productive at lower latitudes (Thorson 1958, 1961; McRoy and Allen 1974). Recent studies of hard bottom (live bottom) habitats on the South Atlantic continental shelf have demonstrated seasonal as well as diurnal/noctural patterns in demersal fish species composition and abundance (BLM 1981). Species diversity and biomass of invertebrates found in these live bottom areas were found not to vary with respect to depth or latitude in the South Atlantic Bight (BLM 1981).

Current Velocity, Waves, and Storms

63. Water circulation plays an important role in structuring estuarine and marine benthic habitats and communities. The combined influences of freshwater inflow, tidal regime, wind, and oceanic forces result in specific patterns of water movement found in any coastal or estuarine system. The circulation of waters within an estuarine embayment or lagoon are responsible for transporting nutrients, plankton, and benthic larvae; flushing wastes from animals and plants; flushing the system of pollutants; controlling salinity; shifting sediments (eroding and deposition); and mixing the water masses (Clark 1974).

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Naturally occurring storms of high intensity and relatively infrequent periodicity, such as hurricanes and tropical storms, may bring about large sudden changes in estuarine and marine benthic structure by sudden mass transport and redistribution of sediments, high wind and wave induced current velocities, and altered salinity patterns (Hayes 1978).

64. Circulation patterns in open ocean waters are dominated by large-scale forces which may have distant origins, such as massive currents like the Gulf Stream or California Current. Major currents of the North Atlantic and Pacific Oceans and the Gulf of Mexico (North Equatorial Current, Florida Current, Gulf Stream, North Atlantic Current, Labrador Current, Arctic Current, California Current, and Alaska Current) are responsible for regulating temperature and salinity in these oceans, which in turn control the currents (Emery and Uchupi 1972; Sverdrup, Johnson, and Fleming 1942) (Figure 3-32). Outwellings or eddies from these major currents onto the outer continental shelf may markedly affect primary production and benthos production in areas where they are known to occur, such as the South Atlantic (Atkinson 1977; Atkinson, Paffenhöfer, and Dunston 1978; Tenore et al. 1978; Hanson et al. 1981). Nearshore water circulation patterns, on the other hand, are largely controlled by tidal height, wind, waves, and land runoff.
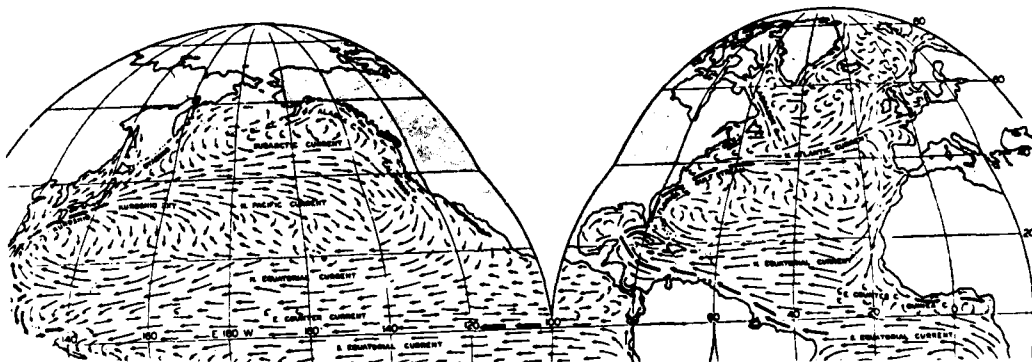

Figure 3-32. Average surface currents of the northern hemisphere of the world's oceans (modified after Sverdrup, Johnson, and Fleming 1942)

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65. Upwelling of cold, nutrient-rich bottom waters onto continental shelves of the east, west, and gulf coasts may enhance productivity and affect benthos secondary production (Carpenter and McCarthy 1978, King 1958). Upwelling on the west coast occurs primarily in the spring and early summer and is usually induced by northerly winds, which through Ekman circulation drive surface waters offshore and cause an easterly movement of bottom waters onto the shelf. Upwelling areas are generally highly localized, and waters come from depths usually less than 200 m.

66. Residual, nontidal, and tidal currents occurring on the continental shelf may significantly modify benthic habitats. The general trend of these bottom currents for the northwestern Atlantic Coast suggest a dominantly southwestward movement, except between Cape Hatteras and Miami (Emery and Uchupi 1972). Large migrating sand waves several meters high are common on the western Atlantic shelf, with movements from northeast to southwest (Emery and Uchupi 1972), suggesting that bottom currents may be a significant factor in sediment transport in some shelf areas. Bottom features such as large sand waves, ripple marks, and degree of bioturbation give evidence of tidal bottom current intensity. Sediment patterns on shelves are controlled by bottom currents that transport sediments from their source areas. Generally the direction and speed of these bottom currents can be inferred from maps of clay and other minerals (Emery and Uchupi 1972). For example, the pattern of sediment grain-size distribution on the shelf of the northwestern Gulf of Mexico indicates a westward flow of bottom waters off Louisiana and a northeastward flow off southern Texas (Curry 1960). The distribution pattern of clay minerals along the entire Atlantic continental shelf indicates the bottom currents move sediments southwestward and into estuaries where general mixing of clays occurs (Hathaway 1972). The general transport of sediments from continental shelves into estuaries means that rivers are only able to contribute sediments to shelf environments during times of flood, when bottom currents are reversed (Emery and Uchupi 1972).

67. Tidal regimes are often the dominant force controlling water

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movement in estuaries. Tidal cycles drive estuarine circulation patterns, and tidal amplitude may vary greatly with latitude as shown in Table 3-7. Within estuarine systems, tidal amplitudes generally decrease from the ocean landward through the inlet to the head of the estuarine basin (Clark 1974). Estuarine bathymetry also influences the magnitude of the water circulation patterns. Flushing rates are greater with increasing tidal range.

68. Circulation patterns in lagoons with little freshwater inflow and somewhat restricted inlet openings are largely controlled by wind. These types of lagoons are often poorly flushed and vulnerable to buildups of contaminants.

69. Current velocities generated by tides, wind, and storms are an important factor in structuring benthic communities associated with estuarine systems. Currents are important in delimiting the distribution of benthic habitat types. Storm-related impacts (disturbance) on benthic communities in soft bottoms may be largely controlled by water depth. McCall (1978) found storm-related disturbance to be a major controlling factor in benthos distribution in Long Island Sound. Current or wave stresses of 0.5 to 1 dyne/cm^2 are capable of entraining most fine-grained sediments from the bottom (Fukuda 1978; Rhoads, Aller, and Goldhaber 1977). Stresses of this magnitude are rare below 20 m (Figure 3-33), and McCall (1978) concluded that the combined stress effects of storms and the tidal system have little influence on the bottom below about 20 m in enclosed waters such as Long Island Sound. The actual depth beyond which wind-generated waves or current stress may disrupt the bottom is a function of the physical dynamics of the particular body of water and may be less than 20 m in a protected estuary or greater than 20 m in an open water body.

   a. Unconsolidated soft bottom habitats. Current velocity affects the distribution of sediment particle sizes in unconsolidated soft bottoms. Coarser sediments are associated with higher current environments, while fine-grained (mud) sediments are associated with lower energy environments. For example, a current velocity of 0.4 knot will shift ordinary sand along the bottom, while a current of 1 knot will shift fine gravel. A

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Table 3-7

Typical Tidal Characteristics of the Coastal Zone of the United States

(after Clark 1974)

Biophysical Region	Type of Tide	Tidal Range, ft			Maximum Tidal Flood	Current Velocity Ebb
		Mean	Spring	Diurnal*		
North Atlantic						
Eastport, Maine (Bay of Fundy)	Equal semidiurnal	18.2	20.7		3.5	3.5
Isle de Haut, Maine (Penobscot Bay)		9.3	10.7		1.6	1.7
Portsmouth Harbor, N. H.		8.7	10.0		1.4	2.1
Boston Harbor, Mass.		9.5	11.0		2.0	1.5
Middle Atlantic						
Dumpling Rocks (Buzzard Bay)		3.7	4.6		0.9	1.3
The Narrows (New York Harbor)		4.5	5.5		2.0	2.3
Cape May Harbor, N. J.		4.4	5.3		2.1	2.5
Virginia Beach, Va.		3.4	0.1		1.3	0.9
Chesapeake Bay						
Wolf Trap Light (lower bay)		1.0	1.2		1.8	2.2
Point No Point (midbay)		1.3	1.5		0.5	0.7
Chesapeake Bay Bridge, Md		0.8	0.9		0.8	1.0
Washington, D. C. (Potomac River)		2.9	3.3		0.7	0.3
South Atlantic						
Wilmington, N. C. (Cape Fear River)		3.6	3.9		2.0	2.7
Savannah River entrance, Ga.		6.9	8.1		1.8	3.0
Mayport, Fla. (St. Johns River)		4.5	5.3		2.5	3.5
Fort Pierce Inlet, Fla.		2.6	3.0		3.0	3.5
Carribbean						
Miami Harbor, Fla.		2.5	3.0		2.2	2.4
Key West, Fla.		1.3	1.6		1.2	2.0
San Juan, P. R.		1.1	1.3		**	**
Christiansted, St. Croix	Diurnal			0.8	**	**
Gulf of Mexico						
St. Petersburg, Fla. (Tampa Bay)				2.3	0.3	0.3
Pensacola Bay entrance, Fla.				1.1	1.8	2.1
Barataria Bay, La.				0.9	1.7	1.7
Aransas Pass, Tex.				1.7	1.6	1.0
Pacific Southwest						
San Diego Bay entrance, Calif.	Unequal semidiurnal	3.9	5.6		1.2	1.4
Monterey Bay, Calif.		3.5	5.3		**	**
San Francisco Bay entrance, Calif.		4.0	5.7		3.3	3.9
Point Arena, Calif.		4.0	5.8		1.3	1.3
Pacific Northwest						
Humboldt Bay entrance, Calif.		4.5	6.4		1.8	2.3
Yaquina Bay entrance, Oreg.		5.9	7.9		2.8	2.6
Grays Harbor entrance, Wash.		6.9	9.0		2.5	2.2
Puget Sound (Elliott Bay), Wash.		7.6	11.3		**	**
Alaska						
Juneau (Gastineau Channel)		13.8	16.4		2.3	2.3
Anchorage (Cook Inlet)		25.1	28.1		3.3	3.3
Goodnews Bay (Kuskokwim Bay)		6.2	8.9		2.6	2.4
Point Barrow		0.3	0.4		**	**
Pacific Islands						
Honolulu, Hawaii (Oahu)		1.2	1.9		†	†
Hilo, Hawaii (Hawaii)		1.6	2.4		†	†
Apra Harbor, Guam		†	†		1.7	3.4
Pago Pago Harbor, American Samoa		2.5	4.0		†	†

* For an unequal semidiurnal tide, the diurnal range is the extreme range over the two sequential tides in slightly over 1 day.

** Weak and variable.

† No data.

Reference: The National Estuarine Inventory; Data source: U. S. Coast and Geodetic Survey.
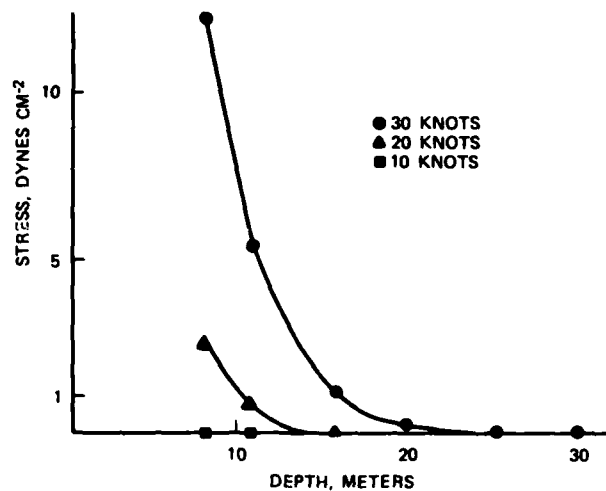
Figure 3-33. Average bottom shear stress as a function
of wind speed and depth along a transect from New Haven,
Connecticut, to Port Jefferson, New York (after McCall
1978)

current of 2.15 knots will move coarse gravel 2.5 cm in
diameter, and 3.5 knots will move angular stones up to
3.8 cm in diameter (note 1 knot = 51.5 cm/sec) (Moore
1958). Therefore, currents largely determine the grain-
size distribution of sediments. Figure 3-34 illustrates
graphically the relationship between current velocity
and its potential to deposit, transport, and/or erode
sediments of various grain sizes. Areas characterized
by high current velocities, such as harbor channels and
coastal entrance channels, usually exhibit an impover-
ished benthic fauna due to the high degree of current
stress associated with these areas. In estuaries and
embayments, filter/suspension feeding groups are found
primarily in higher energy coarse sediment environments,
while deposit feeding benthos dominate the lower energy
mud environments for the most part (Rhoads and Young
1970; Sanders 1958, 1960).

(1) Wave-induced sediment disturbance may be very im-
    portant in structuring shallow estuarine and marine
    benthic communities (McCall 1978; Rhoads, McCall,
    and Yingst 1978; Oliver et al. 1979). It is ex-
    pected that effects of storms with higher wave
    frequencies and subsequent bottom disturbance
    (Figure 3-34) result in patterned distributions
    of benthic communities (i.e., the "spatial mosaic"
    discussed in paragraph 20) in relatively shallow
    (<20 m) shelf environments similar to those

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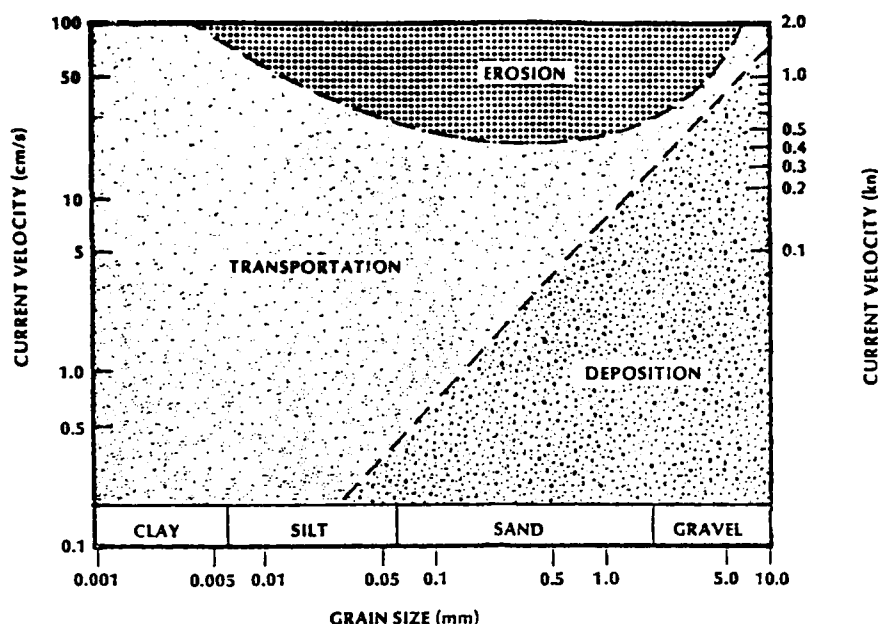
Figure 3-34. The relationship between current velocity and its potential to deposit, transport, or erode sediments of various grain sizes (after Moherek 1978)

observed in estuaries (McCall 1978; Rhoads, McCall, and Yingst 1978). For example, Frankenberg and Leiper (1977) found large spatial and temporal variations in nearshore (<21 m) marine benthic soft bottom community structure on the Georgia continental shelf. Recent studies by Oliver et al. (1980) observed nearshore faunal zonations on the continental shelf off Monterey, California, which were correlated with depth and wave-induced bottom disturbance. Benthos were classified into a shallow zone (<14 m) containing sediments frequently disrupted by wave activity, and this zone was primarily occupied by small, mobile, deposit feeding crustaceans. The deeper zone (>14 m) was dominated by sedentary polychaetes living in permanent tubes and burrows. These variations in faunal structure and animal motility patterns were correlated with water depth and the strength of the wave activity (Figure 3-35). The sedentary, tube-dwelling polychaete dwellers are unable to establish and maintain biogenic structures in areas subject to intense physical sediment movement, and thus they are largely restricted to areas of less intense
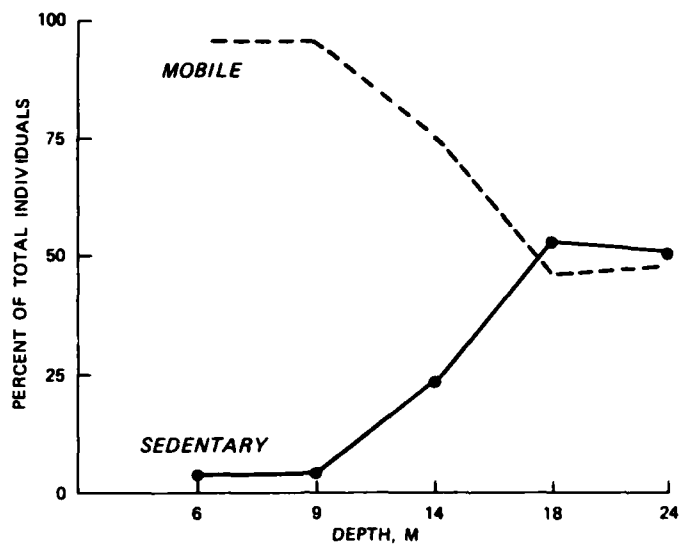
Figure 3-35. Variations in animal motility patterns along
southern sandflats in Monterey Bay, Calif. (after Oliver
et al. 1979)

wave activity (i.e. deeper waters). This same
general pattern of zonations of benthic community
structure in high-energy shallow shelf areas has
also been documented for much of the temperate open
coast of western North America (Carey 1965, 1972;
Lie 1969; Lie and Kisker 1970; Barnard 1963; Van
Blaricom 1978). It is likely that future studies
will identify similar zonations of nearshore (<30 m)
shelf benthos related to high-energy wave-induced
sediment disturbance for the east and gulf coasts
as well (Oliver et al. 1979). European coastal
studies have also documented similar crustaean and
polychaete dominated benthos assemblages related to
wave exposure (Masse 1972; Rees, Nicholaidou, and
Laskaridou 1977).

(2) Adaptive life strategies of benthos associated with
shallow water habitats subject to frequent distur-
bance differ markedly from those faunas character-
istically found in relatively undisturbed soft bot-
toms (see Table 2-1). Communities dominated by
opportunistic species are widespread, but generally
dominate soft bottoms subjected to physical or pol-
lution disturbances (McCall 1978) (see Figure 2-2).
Their distributions are generally patchy in time
and space, reflecting both life history strategies

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and frequency of disturbance. Equilibrium species on the other hand are generally more evenly distributed, reflecting their much lower frequency of disturbance.

b. Aquatic vegetation beds. Currents and storms effectively regulate the distribution and community structure of seagrasses in estuaries and coastal marine environments. Kelp beds, on the other hand, require moderately high wave energies (Phillips 1974). Seagrasses, particularly turtle grass, have been found to be particularly resistant to storm-related stresses, such as hurricanes. Observations by Thomas, Moore, and Work (1961), Oppenheimer (1963), and Phillips (1980) on the impact of hurricanes on turtle grass beds found that winds up to 175 mph (152 kn) had negligible effects on the vegetated beds. Eelgrass may be somewhat less resistant to wave exposure, although this species thrives in moderate current (up to 3.5 kn). Phillips (1972) observed eelgrass beds following a storm in Puget Sound, Washington (1- to 2-m waves for 2 days) with 40-kn winds and found that, although between 7 to 10 cm of sediment was removed exposing the rhizome mat, the eelgrass bed remained intact and subsequently recovered. Seagrass species such as turtle grass and eelgrass are therefore very important sediment stabilizers in shallow estuarine and coastal waters due to their ability to bind sediments and prevent erosion. This was documented by Orth (1977b) following a storm in Chesapeake Bay: up to 20 cm of sediment eroded from unvegetated sand banks, while little, if any, sediment disappeared from within an eelgrass meadow. The density, width, and length of leaves act as baffles that effectively trap sediments. particularly the finer grain sizes (Schubel 1973, Orth 1977a) (see Figures 3-15 and 3-16). Subtle changes in macrobenthos structure may be a consequence of seagrass beds subjected to current stress. O'Gower and Wacasey (1967) found higher numbers of species but lower species diversities and higher dominance (species equitability) in current stressed subtropical seagrass habitats (Figure 3-21).

c. Reefs. Biological reefs (oyster, coral, and sabellariid) require sufficient water movements to maintain their structure. Currents transport the dissolved nutrients, suspended matter, and plankton over the oyster, coral, algal, and worm reefs thereby regulating the production of the reefs. Currents and waves regulate the structure of oyster reef communities (see paragraph 41), and mollusc and sabellariid reefs align themselves with prevailing currents or water movements within the estuarine and marine environment (Figures 2-7 and 2-11). Wave actions modify the shape of

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colonies of individual coral species, and a single spe-
cies may exhibit a number of different growth forms in
varying current and wave energy environments. To main-
tain a flourishing oyster community there must be a
continuous renewal of seawater running over the bottom
(Galtsoff 1964). Adult oysters, living under optimum
salinity and temperature conditions, pump water at a
rate of 15 ℓ/hr. Therefore, oysters cannot exist in
areas of sluggish water in high population densities.
Storms affect the distribution of all reefs by high
current velocities, increased sedimentation rates, and
altered salinity regimes, all of which may adversely
affect the structure of reef communities by physical
removal, burial, or mortalities. Wells (1961) studied
the structure of oyster reef communities following the
passage of three hurricanes in the Newport River, North
Carolina. He found high mortalities in oyster communi-
ties primarily related to the drastically altered salin-
ity regimes, although sediment redistribution and deposi-
tion on reefs also contributed to the mortalities.
Sedimentation was cited by Engle (1948) as a major factor
in oyster mortalities observed in Louisiana, Mississippi,
and Alabama following a hurricane. Storms may also tem-
porarily increase the diversity of coral species by
localized disturbances (i.e., heavy sedimentation and
physical abrasion), which open up bare substrates for
colonizing fast growing "opportunistic" species. These
areas will then undergo a localized succession, and the
opportunistic coral and algal species will be gradually
replaced by slower growing but more highly competitive
species (Grassle 1973; Rogers, Suchanek, and Pecora
1982); storm-related disturbances thereby create spatial
mosaics in coral reef community structure not unlike
those observed in unconsolidated soft bottoms. In
coastal marine environments, a particularly important
role that coral and sabellariid reef habitats serve is
that of shoreline stabilization by breaking up and dis-
sipating wave and current energies nearshore.

d. Rock/hard bottom habitats. The persistence of this habi-
tat type and its associated communities is largely de-
pendent on current and/or wave energies sufficiently
strong enough to maintain a sediment-free surface. Fau-
nas of this habitat type are especially sensitive to
large storms and high current velocities which may in-
crease sedimentation rates and suspended solids levels
to unacceptable levels smothering filter/suspension
feeding species, or physically dislodging attached
sedentary forms from their hard substrates. Studies
relating the growth of particular fouling species to
current velocity may serve to illustrate the importance

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of current stress to epifaunal invertebrates (Figure 3-36). When currents are too low, hard bottom community species do not receive enough food and aeration for internal metabolic activities and waste removal. Alternatively, when currents are too high the stress of attachment, feeding, and maintenance diminishes the amount of biological structure that can be maintained.
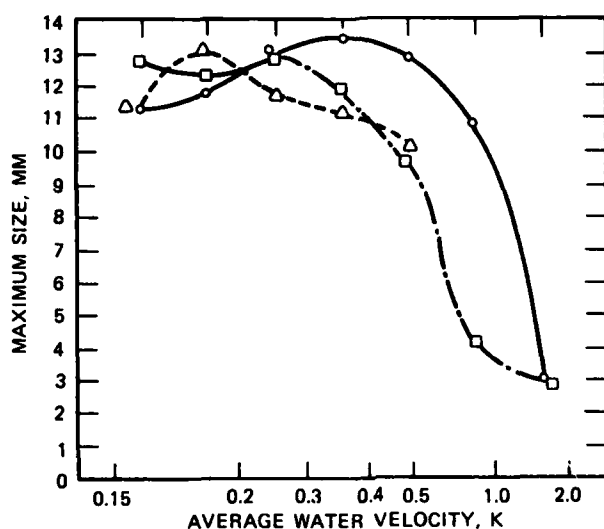
Figure 3-36. Current velocity effects on the growth of three species of barnacles, *Balanus amphitrite* (circles), *B. improvisus* (squares), *B. eburneus* (triangles) (after Doochin and Smith 1952)

Depth

70. The bathymetry of a particular estuarine basin, coupled with freshwater inflow and tidal range, will determine the particular water circulation properties and types of substrates found. The significance of depth in regulating the frequency of physical disturbances to substrates has already been discussed (paragraph 69). In deep estuaries such as fjords, depth may also influence the standing crop of benthos found, although substrate quality changes also occur which may be a contributory factor. Figure 3-37 illustrates this relationship for an

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Figure 3-37. Macrobenthic infaunal biomass distribution according to (a) depth in a high-arctic fjord and (b) substrate quality in a tropical fjord (after Thorson 1957). Note: all biomass units are expressed as grams (G) per square meter

arctic fjord (Thorson 1957). There appears to be some relative de-
crease in benthic infaunal biomass with increasing depth and distance
upstream from the mouth of the estuary. In coastal marine shelf
environments, benthos community structure, species diversity, and
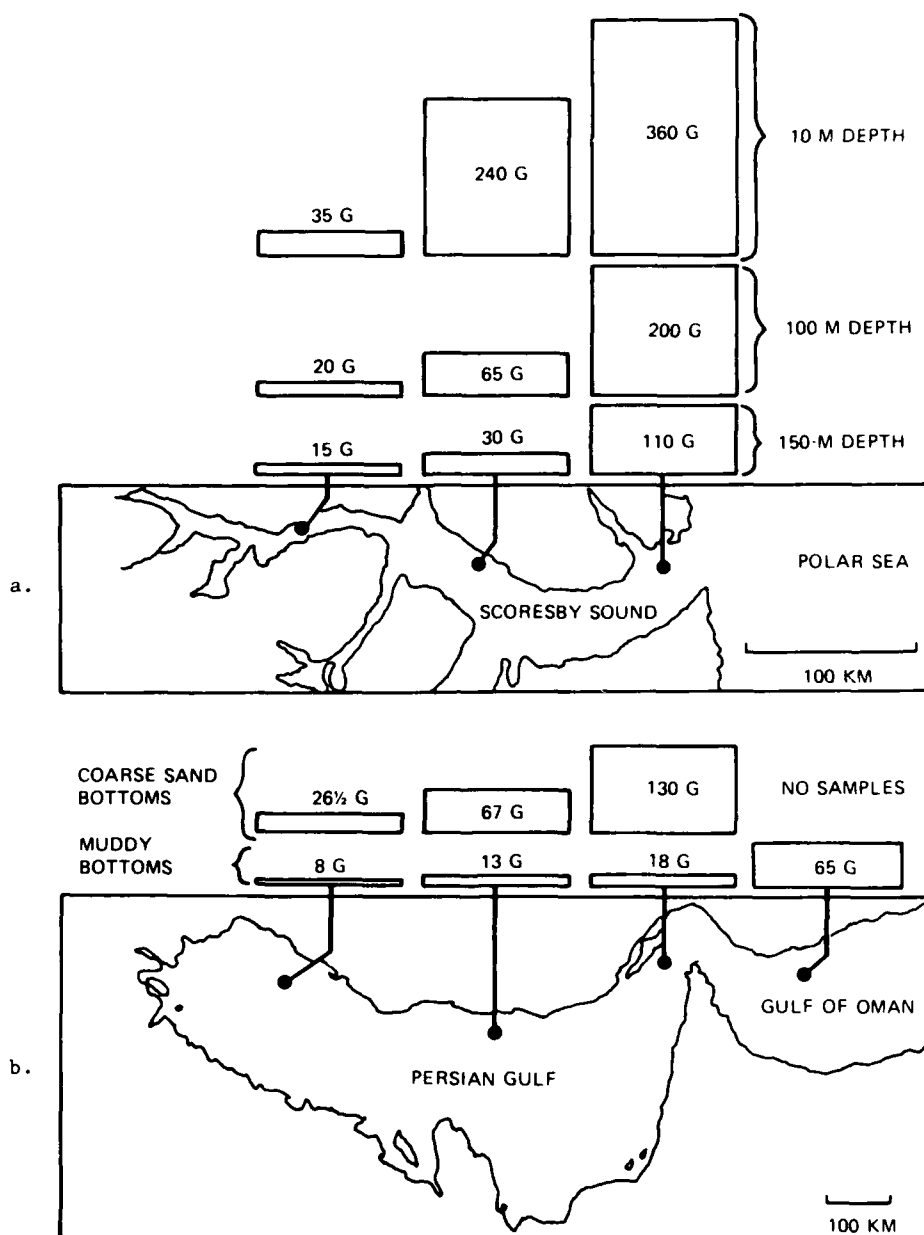standing crop also show generalized trends with depth. Studies have
described a general species continuum of change along depth gradients
from shallow water (20 m) to deep abyssal regions (Parker 1964; Sanders
1968; Sanders and Hessler 1969; Rowe, Polloni, and Horner 1974; Flint
and Holland 1980). On a macroscale, benthos standing crop generally
decreases from higher to lower latitudes and from nearshore shelf to
outer shelf regions (Figure 3-38) as a consequence of decreasing pri-
mary production and food resources (Figure 3-39) (Emery and Uchupi 1972;
Rowe, Polloni, and Horner 1974; Haedrich and Rowe 1977; Mills 1980).
At depths of 1000 m or greater, benthos standing crop becomes relatively
uniform and no latitudinal gradient is apparent (Figure 3-38). These
trends are highly generalized, and localized variations in primary
production (i.e. upwelling) for a region may alter this general pattern
in the shelf environment. For example, an inverse depth-related dis-
tribution of macrobenthic biomass has been observed on the Georgia
continental shelf (Figure 3-40) (Tenore et al. 1978, Hanson et al.
1981) and on the Washington continental shelf (Lie 1969). Tenore et al.
(1978) found a relatively impoverished marine benthic community at
nearshore shelf stations, which they attributed to low nutrient inputs
and unfavorable sedimentary regimes. Nitrogen-rich Gulf Stream intru-
sions onto the shelf are common and may be responsible for the higher
standing crops observed at outer shelf stations due to higher primary
productivity in those areas (Tenore et al. 1978, Hanson et al. 1981).
Flint and Holland (1980) identified three depth-related benthic in-
faunal assemblages in a transect study off the south Texas coast. Spe-
cies diversity and equitability increased from shallow (22-m), middepth
(36- to 49-m), to deepwater (78- to 131-m) shelf areas, primarily as a
response to increased environmental stability. They concluded that
environmental heterogeneity, including climatic variability (current
velocity, waves, temperature, salinity), may be most important in
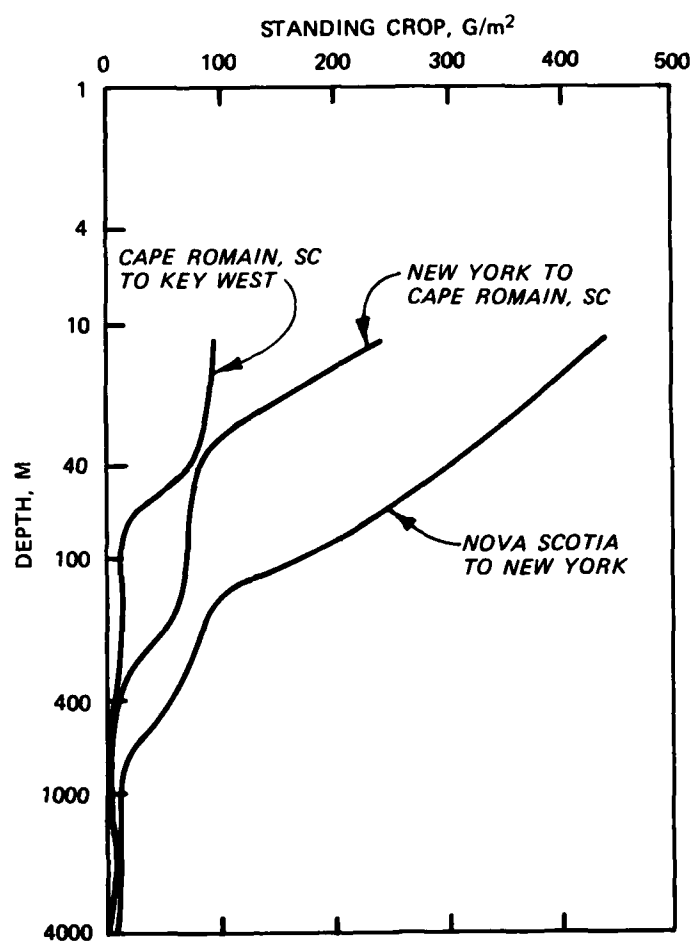
Figure 3-38. Highly generalized distribution gradients with depth of
macrobenthos standing crop biomass for three latitudinal ranges of
the ocean floor off the northwestern Atlantic coast (after Emery and
Uchupi 1972)

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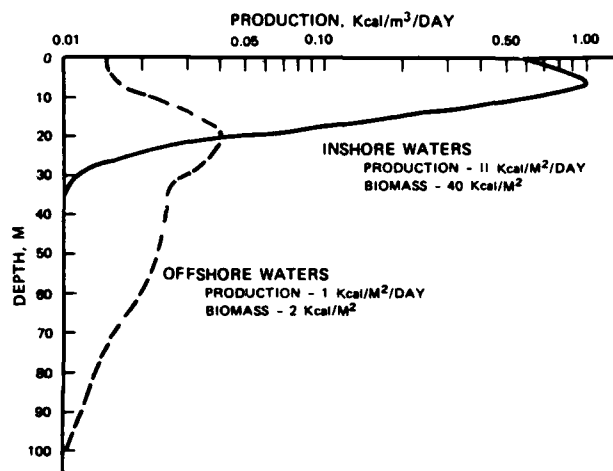
Figure 3-39. Comparison of the vertical distribution of primary production and biomass between inshore and offshore waters of the northeast Atlantic (after Currie 1958)
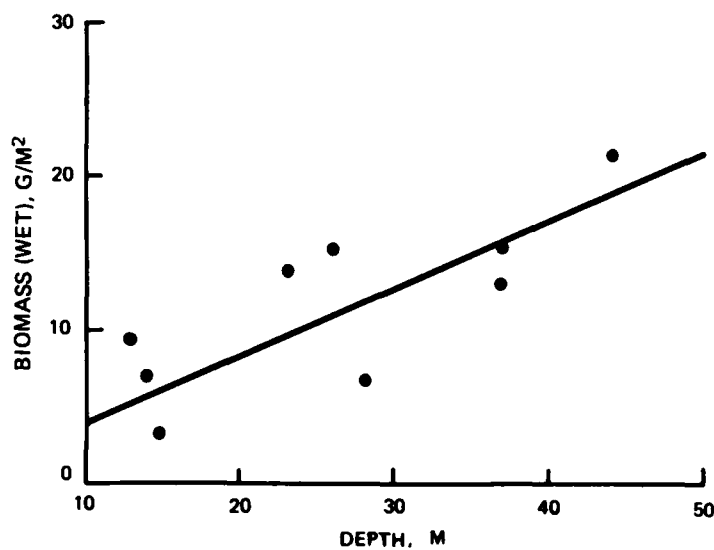
Figure 3-40. Scattergram and plot of a significant (p < 0.05) regression line illustrating the relationship of macrobenthic biomass and depth across the Georgia continental shelf environment (data from Tenore et al. 1978)

controlling shallow-water benthos structure, while species interactions become progressively more important with increasing environmental stability (i.e. depth). Others have made similar observations and reached similar conclusions concerning the structure of benthic communities in nearshore and offshore shelf environments of the west and east coasts (Sanders 1968; Sanders and Hessler 1969; Day, Field, and Montgomery 1971; Boone, Granat, and Farrell 1978; Jumars and Fauchald 1977). Studies of benthic trophic structure along a gradient of increasing depth have shown some general trends. For example, Parker (1964) found decreasing compositions of suspension/filter feeding benthos and increasing compositions of deposit feeding benthos with increasing depth off California from shallow shelf to abyssal environments (Figure 3-41). Substrate instability due to wave-induced disturbance may alter this pattern in nearshore shelf areas along high-energy coastlines (see paragraph 69a(1)) (Figure 3-35).

a. Unconsolidated soft bottom habitats. The trends outlined in the previous paragraph are all apparent in soft bottom habitats. Depth-related changes in sediment composition are also apparent. It is generally believed that environmental heterogeneity (i.e., difference in substrate, current velocity, temperature, dissolved oxygen, salinity, etc.) is primarily responsible for controlling benthic community structure (i.e., these are "physically accommodated communities") in temporally variable estuarine and shallow marine environments; whereas biological interactions become increasingly more important in environmentally stable environments (i.e., these are "biologically accommodated communities") (Sanders 1968, 1969). Thus, depth indirectly influences community structure by dampening or magnifying the variability of the other habitat descriptors, which in turn delimit the distribution and abundance of benthic species associated with soft bottoms.

b. Aquatic vegetation bed. Decreasing light attenuation with depth sharply limits the seaward distribution of submerged attached marine macrophytes (seagrasses and algae). The compensation depth is limited by turbidity and generally increases with distance from shore, and all submerged aquatic vegetation bed habitats are generally restricted to depths of 31 m or less. Figure 3-42 illustrates the distribution of eelgrass and dominant bivalve species with depth and substrate

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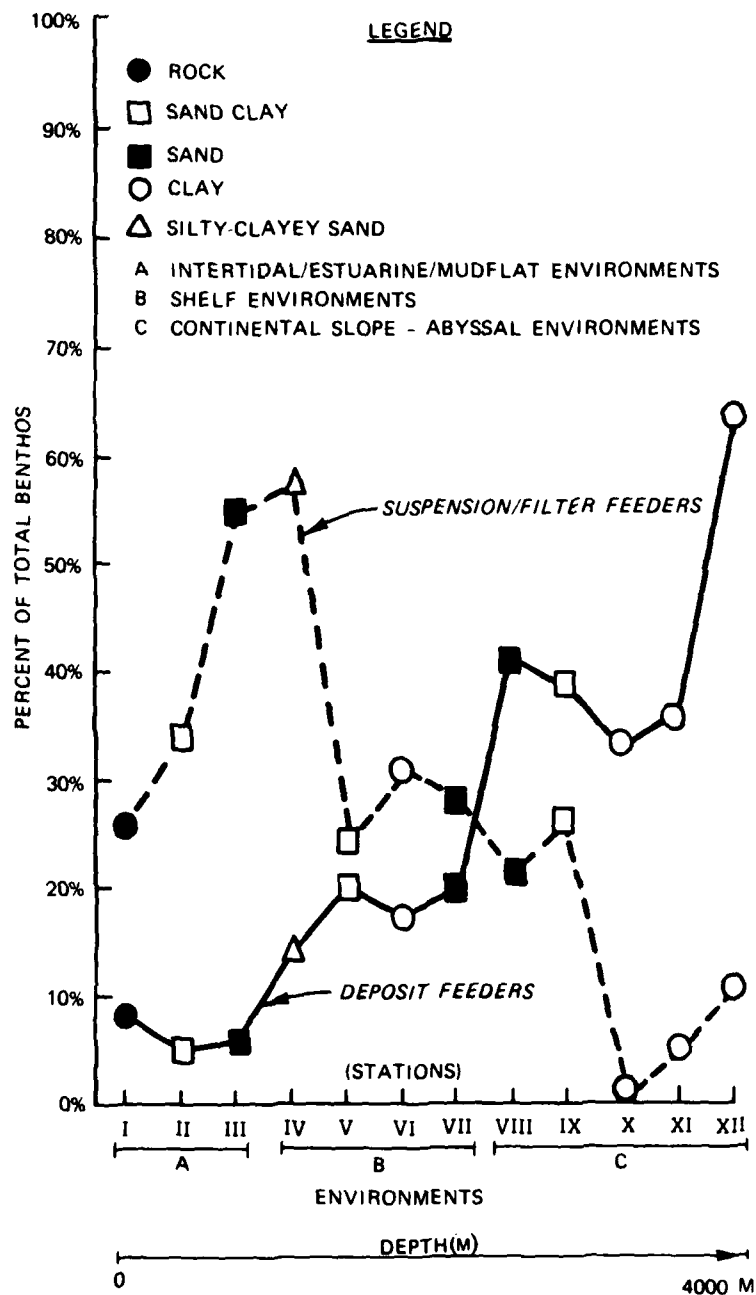
Figure 3-41. Distribution of two benthic feeding types in various
sediment types along a gradient of increasing depth (after Parker
1964)

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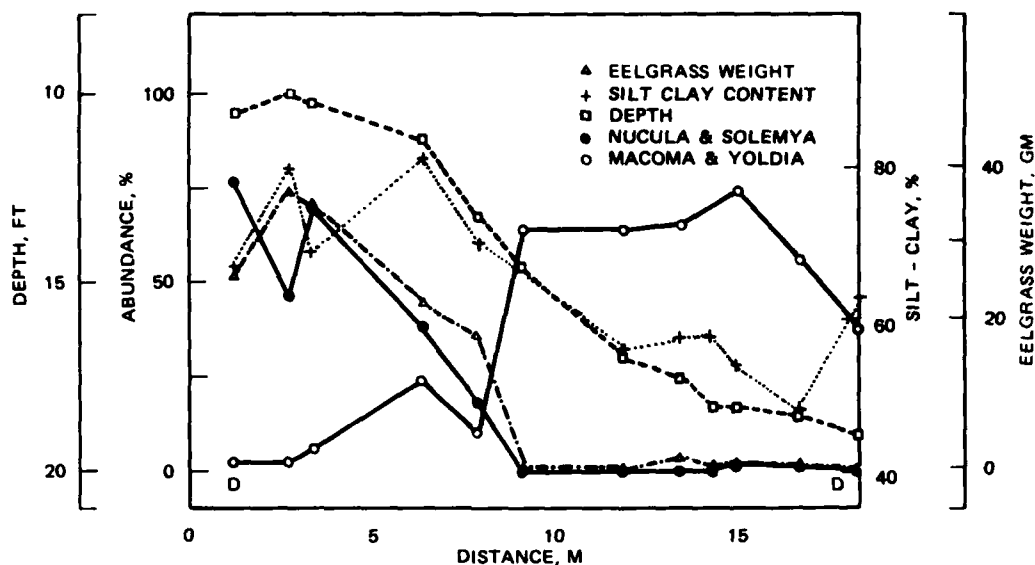
Figure 3-42. Distribution of dominant bivalve species, water
depth, dry weight of eelgrass (per 0.1 m^2), and percent silt-
clay along a transect (after Levington 1977)

quality (silt-clay content) in a Massachusetts estuary.

c. Reef habitats. Reef habitats are sharply delimited by
    depth, particularly true coral reefs. Symbiotic zoo-
    xanthellae require high light intensities, thereby
    restricting the depth regions of active coral growth to
    the upper 30 m or so from the surface. Other reefs
    such as sabellariid worm reefs are limited to rela-
    tively shallow nearshore high-energy environments
    between 2 and 10 m.

d. Rock/hard bottom. This habitat is not depth limited,
    but is found whenever currents and wave activities are
    sufficient to maintain a clean, sediment-free surface.
    Benthic community dominants are generally sessile.

Water Quality

71. Water quality is of the utmost importance to all aquatic or-
ganisms. Various discrete, measurable aspects of water quality, such
as salinity and temperature, have already been discussed as important
parameters structuring estuarine and coastal marine benthic communities.

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Therefore, this section will focus on a few important water quality parameters such as dissolved oxygen, turbidity, and general pollution which may significantly affect benthic community structure and function within estuarine and coastal marine environments.

Dissolved oxygen

72. Dissolved oxygen has long been shown to be a significant factor in delimiting the distribution of benthic faunas in aquatic environments. In seasonally stratified estuaries, such as Chesapeake Bay, seasonally hypoxic or anoxic conditions developing near the bottom have been observed to locally extinguish the benthic faunas occurring there (Biggs 1967; Holland, Mountford, Mihursky 1977; Taft et al. 1980). Fine-grained sediments with high organic matter content may lead to hypoxic or anoxic conditions in sediments and overlying waters. Oxygen depletion at the water-mud interface may result in complex changes in the solubility or concentrations of many elements basic to biological productivity (May 1973). Under anaerobic conditions, desorption of phosphate, hydrogen sulfide, carbon dioxide, ammonia, silicate, iron, and other metals may take place (Jitts 1959, Mortimer 1971). In strongly reducing environments desorbed metals generally form highly insoluble metal sulfides and precipitate out of solution; but these metals may be remobilized by processes such as sediment resuspension and/or bioturbation (e.g. by burrowing infaunas) of reoxidizing sediments (Troup and Bricker 1975). Oxygen depletion in sediments following a disturbance or pollution event may displace resident benthic species (equilibrium species) in favor of eurytopic opportunistic species (see Figure 2-2). May (1971) found 100 percent mortality in oysters from a reef in Mobile Bay following a 10-day period of low dissolved oxygen. Anoxic conditions resulting from a serious outbreak of the red tide organism *Gymnodinium breve* were responsible for the defaunation of benthos on the Florida west coast in Tampa Bay (Simon and Dauer 1977). Dissolved oxygen levels are generally not limiting to marine benthic communities except in areas subject to (a) seasonal thermoclines or haloclines (e.g., the Louisiana shelf), (b) upwellings, (c) nutrient enrichment from anthropogenic sources (sewage sludge), and

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(d) large algal blooms (red tide). Oxygen depletion has been observed in the New York Bight in deeper areas below the seasonal pycnocline (temperature-related density gradient) at about 30 m (Boesch 1982, Malone 1978). A prolonged period of anoxia or hypoxia may lead to faunal extinctions in benthic habitats where they occur.

73. Nutrient levels in marine coastal environments generally decrease from nearshore to offshore and affect the primary production and benthic secondary production (Figures 3-38 and 3-39). Localized nutrient enrichment from natural or anthropogenic sources may increase benthic productivity. Tenore et al. (1978) and Hanson et al. (1981) attributed higher macrobenthos standing crops on the outer continental shelf to nutrient enrichment from Gulf Stream intrusions onto the Georgia shelf (Figure 3-40). Upwelling of slope water onto the outer continental shelf may be the primary source of inorganic nutrients in these areas (Carpenter and McCarthy 1978), while benthic regeneration of nutrients may be the primary source in estuaries and bays (Nixon, Oviatt, and Hale 1975). Offshore disposal of sewage sludge increases sediment nutrient levels and organic carbon content which may enhance benthos secondary production. A sewage sludge enriched area in the New York Bight apex is reported to support higher standing crops of macrobenthos than surrounding unaffected areas and nearby estuaries and bays, although the quality of the macrobenthos in the enriched area to demersal fish predators is questionable (McGrath 1974, Boesch 1982). An analysis of benthos structure in the enriched area and local fish feeding habits by Boesch 1982 suggests that only a small fraction of the resident benthos in the enriched areas is being utilized as prey by demersal predators, and that the overall trophic resource potential of the area may be reduced. High benthic standing crop biomass does not imply predator utilization, and may be instead the result of low-level predator cropping (Virnstein 1977, 1979; Reise 1977).

Turbidity

74. Turbidity is an expression of an optical property of a fluid caused by the presence of suspended matter such as clay, silt, finely divided organic and inorganic matter, plankton, and other microscopic

organisms. Increased turbidity and suspended solids loads in estuaries generally result in increased sedimentation, which affects benthic habitats. In estuaries, flocculation of silt-size particles generally takes place at the river estuary boundary (0-5 ^{o}/oo) and is dependent on temperature, pH, and the types of sediments in suspension.

75. Studies of sedimentation in benthic communities such as oyster reefs have shown that deposits of silt or loose sediments as thick as 1 to 2 mm over a hard substrate or shell surface are sufficient to cause failure of setting oyster larvae and other larvae (Galtsoff 1964). Increased sedimentation in bays and estuaries has destroyed oyster reefs along the Texas coast (Galtsoff 1964) as a result of anthropogenic influences (soil erosion, deforestation, population increases).

76. Turbidity levels in water influence the depth of light penetration, which in turn affects the ability of plants to carry out photosynthesis. The depth at which oxygen production from photosynthesis equals oxygen consumption through respiration defines the compensation point; the compensation point in turn is approximately equal to that depth at which light penetration is 1 percent of the surface intensity. Water transparency or turbidity affects the compensation depth, which varies from less than 1 m in turbid estuaries to over 100 m in the nutrient-poor open ocean and decreases shoreward as a function of increased nutrient levels and primary production (Raymont 1963). High turbidity restricts the euphotic zone in estuaries, while suspended materials enhance the photosynthetic rate by providing large quantities of nutrients (Stern and Stickle 1978). Turbidity levels generally decrease from inshore to offshore except in areas of nutrient enrichment (upwelling, intrusions, sewage sludge disposal, etc.). Tenore et al. (1978) found a general decrease in suspended particulate matter offshore as a result of seawater dilution of coastal-derived suspended solids within the Georgia Bight (continental shelf). The depth distributions of aquatic vegetation bed habitats are turbidity limited. The maximum depth reported for kelp beds is around 31 m, while seagrasses such as eelgrass and turtlegrass are rarely found

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below 10 and 20 m, respectively, in low-turbidity waters (Phillips 1974, 1978, 1980; Zieman 1975). Large benthic macrophytes such as kelp and seagrass beds may baffle currents, thereby trapping sediments and lowering turbidities. Filter/suspension feeding benthos such as oysters, other bivalves, barnacles, and tunicates may also play an important role in reducing turbidities by filtering suspended solids from the water column and depositing the material as feces and pseudofeces (Haven and Morales-Alamo 1967). Haven and Morales-Alamo (1967) found that oysters may produce up to 2422 kg/hectare/week of pseudofeces and feces. These biodeposits were found to consist of particles generally less than 3 μ in diameter, and were between 77-91 percent inorganic matter and between 4-12 percent organic carbon. Other types of benthos, such as surface feeding species, may increase near bottom turbidity levels as a result of their feeding activities (Rhoads 1973). Pumping rates in filter/suspension feeders are frequently reduced during periods of high concentrations of suspended solids which clog the animal's filtering apparatus. When turbidity levels remain at high levels, a filter feeding organism's growth rate will be reduced (Stern and Stickle 1978). Coral reef habitats are particularly sensitive to turbidity and siltation (Grigg 1970, Bok 1978). The effects of turbidity and suspended solids on aquatic organisms and associated environmental impacts have been extensively studied and reviewed under the Dredged Material Research Program (Stern and Stickle 1978; Hirsch, DiSalvo, and Peddicord 1978; Peddicord and McFarland 1978). These studies generally found that most species survived short-term levels of suspended solids associated with normal dredging and disposal operations, and that long periods of exposure were generally required to cause mortalities. Furthermore, contaminants bound by sediments are generally not readily available to biota (Luoma 1974; Kendall 1978; Windom and Kendall 1979; Neff, Foster, and Slowey 1978; Stern and Stickle 1978; Hirsch, DiSalvo, and Peddicord 1978; Peddicord and McFarland 1978), due to strong sorption by organic particulate matter and clay minerals. Dissolved contaminants rather than sediment-bound contaminants appear to be the major pathway for bioaccumulation and toxicity in aquatic organisms.

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Pollution

77. A comprehensive discussion of pollution effects on benthic communities is beyond the scope of this report. Much has been written in recent years concerning individual pollutants and their effects on aquatic organisms. Pollutants may be in the form of organic (sewage, hydrocarbon, pesticides) or inorganic (metals, radionuclides, chemicals) contaminants. Recent reviews by Reish et al. (1979); Pearson and Rosenberg (1978); Pearson 1982; and Pearson, Duncan, and Nuttall (1982) summarize much of the extensive pollution literature as it relates to estuarine and marine taxa, individual species, and benthic community responses. The Environmental Protection Agency's "Quality Criteria for Water" (Red Book) reviews the literature and critical levels for a number of priority pollutants, although a recent review of the Red Book by Thurston et al. (1979) has questioned the adequacy of critical levels established for many of the priority pollutants. In estuaries, the degree of eutrophication may have a significant effect on the toxicity and stimulatory and/or inhibitory effect of a given contaminant or group of contaminants at the population or species level. It is well known that dissolved organic carbon, suspended particulate organic matter, and clay minerals will chelate metals and organic pollutants and thereby alter and frequently reduce their toxicity and bioavailability (Luoma 1974; Linberg, Andren, and Harriss 1975; Smith 1976; Windom 1975; Kendall 1978; Neff, Foster, and Slowey 1978). Therefore, pollutants may be more toxic and/or bioavailable in oligotrophic aquatic environments than in eutrophic environments such as estuaries. This has been demonstrated for mercury, copper, and sewage pollution (Lewis, Whitfield, and Ramnarine 1972, 1973; Luoma 1974; Kendall 1978; Dauer et al. 1979; Dauer and Conner 1980).

78. Organic pollution as a result of nutrient enrichment from sewage effluents in low to moderate amounts may enhance the primary and secondary production of an aquatic system. Severe eutrophication from sewage sludge may increase the nutrient loads in the water column beyond a system's capacity to assimilate them. This nutrient overload stresses animal communities in these systems by lowering dissolved

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oxygen (DO) levels and increasing biological and chemical oxygen demand. Lower DO levels may (a) in turn destabilize a community by reducing the species diversity and equitability to produce high dominance and (b) alter the productivity compared with a more natural, unenriched area. Sensitive, stenotopic species are selected against in favor of eurytopic, opportunistic species able to exploit marginally suitable habitats (Table 2-1). A classic example of severe water pollution was caused by duck farms in Long Island, New York, where indiscriminate dumping of duck manure into the bay resulted in an excessive buildup of nitrogenous wastes and large plankton blooms and a subsequent decline in shellfish populations in this area (Reidfield 1952, Ryther and Dunstan 1971). Organic pollutants such as sewage effluents and/or sludge have been much studied and their effects on benthos described. In general, four benthic faunal response zones are recognized as surrounding an organic effluent source (Reish 1973). The first zone, which is closest to the effluent source, is abiotic (grossly polluted); macrofauna are absent from this zone due to hypoxic or anoxic conditions. At a greater distance there exists a polluted zone characterized by a few very tolerant species; exploitation of enhanced organic material by a few eurytopic species may result in high population densities for these species. A third zone, lying between the polluted and normal zone, has been termed the enriched, hypertrophic, or transitory zone (Pearson and Rosenberg 1976, 1978; Reish 1973). In this zone the number of species, densities, and biomass may be increased above levels found in the normal, unaffected fourth zone. (See Figure 2-2 for a representation of a soft bottom benthic community's response to a pollution distance gradient.)

79. A study by McIntyre (1977) indicated that carbon input rates to the subtidal benthos were 55 times the natural rate at a sewage dump site. The enriched site had higher invertebrate densities ($47,285/m^2$ versus $1310/m^2$) and biomass (129.9 g/m^2 versus 40.5 g/m^2 wet weight) than a similar but unaffected site, although the number of species found was lower at the enriched site (20 versus 33 species). A biostimulatory effect was also found in a study by Dauer and Conner (1980)

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in Tampa Bay. They found individual polychaete densities, total bio-mass, and individual species numbers significantly greater at a mod-erately sewage-affected site.

80. Nutrient enrichment in the form of sewage effluent may have a biostimulatory effect, especially in nutrient-poor environments such as the open ocean (Dauer and Conner 1980). The greatest enhancement of biological productivity will occur within coarser sandy sediments com-pared to naturally organically rich, high clay-silt-content sediments. Dauer et al. (1979) found little enhancement of benthic productivity from sewage effluent in clayey-silt-type sediments, while Dauer and Conner (1980) found an almost four-fold increase in benthic productiv-ity in sediments with low concentrations of fine-grain-size particles (2.67 percent silt-clay; 0.68 percent organic matter). Orth (1977b) found a similar relationship for eelgrass, Zostera marina, in low silt-clay-content sediments artificially enriched with fertilizer.

81. Environmental contamination from sewage and industrial ef-fluents with metals, pesticides, PCB's, organic sludge, oil pollution, and radioactive wastes may adversely impact animal and plant communities by acute and chronic toxicity stress and by degrading habitats (Reish et al. 1979; Pearson and Rosenberg 1976, 1978). Synergistic or antago-nistic effects of multiple contaminants may further compound the poten-tial environmental impacts. Sublethal chronic effects of low-level exposure to multiple pollutants are not well understood (Malins and Collier 1981). Studies have shown that the effects of multiple pollu-tants in combination may be additive and consequently much more severe (Gray 1974, 1976; Braek, Jensen, and Mohus 1976; Vernberg, DeCoursey and O'Hara 1974). On the other hand, studies of estuarine benthos in Southwest England subjected to chronic metals pollution for 200 years from mining operations have demonstrated the remarkable ability of benthic communities to survive and adapt to toxic metal stresses; these communities show little discernible change in structure compared to nonmetal-contaminated estuaries (Bryan 1971, 1973, 1974; Bryan and Hummerstone 1971, 1973a, 1973b, 1977). Although the distribution and diversity of species in these heavily contaminated estuaries is fairly

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normal, organisms found there are heavily contaminated with metals, and tissue concentrations may range two to three orders of magnitude higher than those from uncontaminated estuaries; these organisms may thus represent a potential hazard to man (Bryan 1974). Although food web-mediated bioamplification of contaminants has been demonstrated in terrestrial ecosystems (Woodwell, Wurster, and Isaacson 1967; Rudd, Craig, and Williams 1981), attempts to document its occurrence in aquatic ecosystems have generally failed except possibly in the case of mercury (Kendall 1978; Pentreath 1976a, 1976b, 1976c; Windom et al. 1976a; Windom and Kendall 1979; Gardner et al. 1975; Gardner et al. 1978; Irukayama 1967; Eisler 1978; Jernelöv and Lann 1971; Stickney et al. 1975; Huckabee and Blaylock 1972). The efficiency of food web transfers of mercury to predators may be largely a function of the chemical form of mercury in the prey. Jervelöv and Lann (1971) demonstrated preferential assimilation of methylmercury and excretion of inorganic mercury in fish. Analysis of benthos and nekton by Kendall (1978) have shown that infaunas generally contain relatively low levels of methyl-mercury (MeHg) (<30 percent) relative to predacious nekton species from the same areas. Others have verified this from other aquatic systems (Jernelöv and Lann 1971, Luoma 1974). Therefore, low transfer efficiencies of mercury are expected in fish feeding predominately on benthic invertebrate prey with low methylmercury body burdens. On the other hand, tertiary consumers feeding predominately on fish have been found to exhibit higher mercury-retention efficencies because their teleost prey generally contain high levels of methylmercury relative to their total mercury burden (70-100 percent) (Rivers et al. 1972, Westöö 1973, Bishop and Neary 1974, Stickney et al. 1975, Gardner et al. 1975, Gardner et al 1978, Windom et al. 1976b). This was experimentally verified by Pentreath (1976c) who found low assimilation of inorganic mercury by the Plaice Pleuronectes platessa fed inorganic mercury (203 Hg) labeled Nereis, and high assimilation efficiencies from organic mercury (203 MeHg) labeled Nereis. Therefore, as levels of methylmercury increase in prey relative to their total mercury burden, the efficiency of food web-mediated mercury transfers from prey to

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predator species is expected to increase. This is illustrated in a study by Windom et al. (1976a), who found higher mercury but lower cadmium transfer efficiencies at higher trophic levels in marine fish collected from the Georgia embayment (continental shelf) (Figure 3-43).
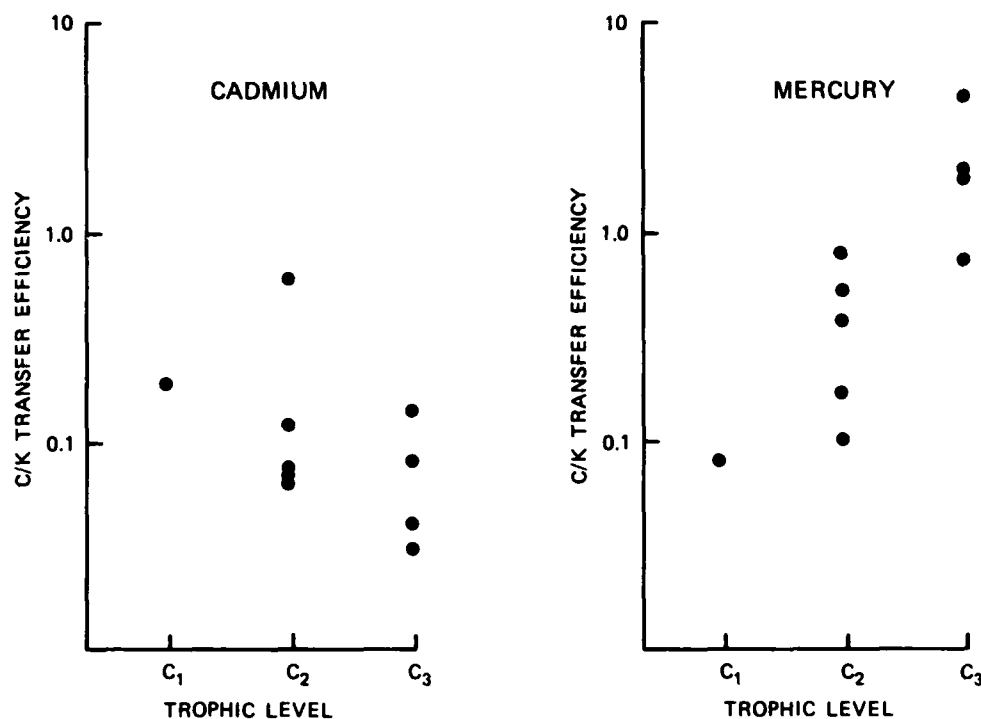
Figure 3-43. Cadmium and mercury transfer efficiencies in Georgia embayment food chains (after Windom et al. 1976a) (see Windom et al. (1976a) for an explanation of transfer efficiency (C/K) determinations)

Jernelöv and Lann (1971), summarizing experimental results from Sweden, found bottom feeding fish (i.e. invertebrate predators) assimilated less than 25 percent of their total mercury burden through the food web and the rest directly from the water. They found fish-eating aquatic predators accumulated as much as 60 percent of their total mercury burdens from their food (fish) and the remaining 40 percent directly from the water. Other studies have also demonstrated that food chain uptake of mercury may account for a significant percentage of the total

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mercury body burden observed in fish (Huckabee and Blaylock 1972; Ratkowsky et al. 1975; Pentreath 1976a, 1976b, 1976c; Windom et al. 1976a). Therefore, conditions which promote or enhance the production and formation of monomethylmercury from inorganic mercury in aquatic ecosystems (Bisogni 1979) will lead to greater mercury bioaccumulation at lower trophic levels and subsequent potential biomagnification of mercury at higher trophic levels. Recent studies in Swedish lakes have found a negative correlation between methylmercury production and pH, with higher rates of monomethylmercury production at a lower pH (Landner and Larsson 1972; Jernelöv, Hansson, and Linse 1976; Hultberg 1977; Beijer and Jernelöv 1979). The rate of methylmecury formation is dependent on microbial activity and the bioavailability of mercury in sediment-bound versus dissolved forms (Jenson and Jernelöv 1969, Jernelöv 1970). The pH of the water will also determine whether mono- or dimethylmercury will be the dominant compound formed. Of the two forms, only monomethylmercury shows a strong affinity for biological tissue, the other being relatively innocuous in aquatic systems (Wallace et al. 1971; Kolb, Porcella, and Middlebrooks 1973). Mercury concentrations accumulated in biota as methylmercury may vary appreciably in different aquatic environments subjected to similar levels of pollution, but varying levels of eutrophication. Oligotrophic environments generally exhibit higher levels of methylmercury in resident biota than eutrophic environments (Beijer and Jernelöv 1979, Luoma 1974). Eutrophic aquatic environments such as estuaries generally exhibit higher pH's which may favor volatile dimethylmercury formation and a higher production of organic matter, which complexes the mercury thereby reducing its bioavailability. It should be apparent from the preceding discussion that complex processes govern the formation of organic and inorganic mercury species in aquatic environments, which formation in turn affects the observed environmental distributions and assimilation efficiences of mercury in biota at any given location. Other metals also exhibit complex chemical forms which affect their distribution and availability to biota (Wood 1974).

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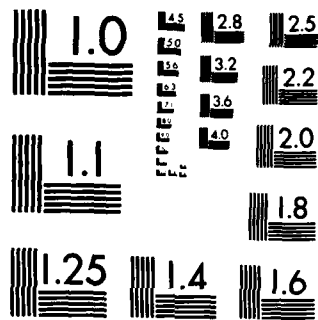
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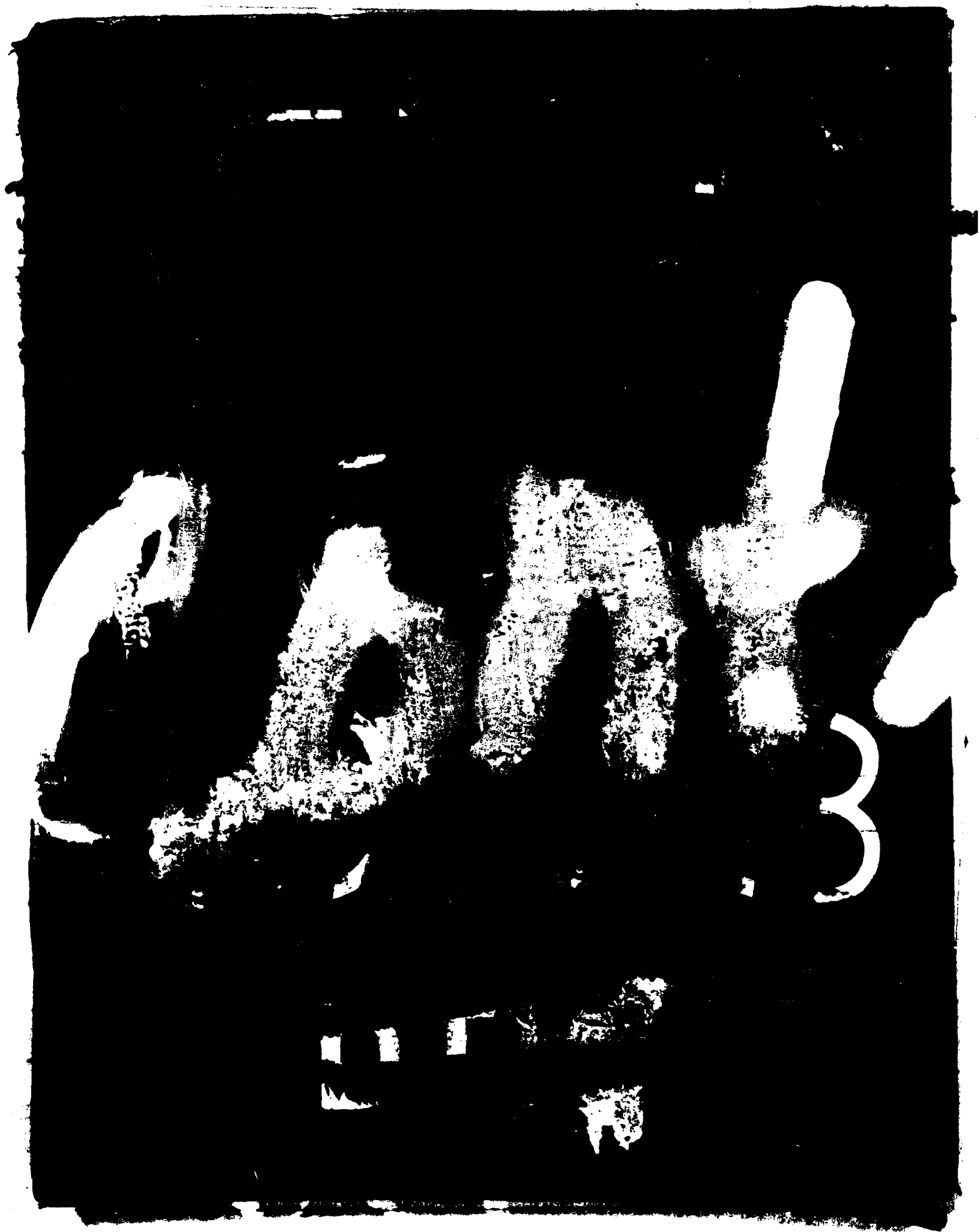
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Errata Sheet

No. 1

THE ROLE OF PHYSICAL-CHEMICAL FACTORS IN STRUCTURING

SUBTIDAL MARINE AND ESTUARINE BENTHOS

Technical Report EL-83-2

June 1983

1. Page 78, Figure 3-22: Replace title for Figure 3-22 with

> Figure 3-22. Seasonal distribution of water
> temperature, *Zostera* dry-weight biomass, mean
> epifaunal and infaunal densities, and major
> fish species biomass (adapted from Vernberg
> 1981)

2. Page 86, Figure 3-27: Replace title for Figure 3-27 with

> Figure 3-27. The generalized metabolic response to temperature
> of animals from different climatic regions (adapted from
> Vernberg 1981)

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